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AN ABSTRACT FOR THE THESIS OF Nancy Ellen Broshot for the Master of Science in Biology presented November 23, 1982.

Title: The Effect of Dwarf Mistletoe (Arceuthobium americanum) upon a Portion of the Carbon Budget of Lodgepole Pine (Pinus contorta).

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Arceuthobium americanum is a vascular plant which is parasitic upon Pinus contorta var. murrayana. Its documented effects include reductions in host growth, vigor and wood quality. The specific physiological changes that occur in the host are, for the most part, unknown.

In an attempt to understand the manner in which the mistletoe alters its host's carbon budget, a model is proposed which states that the host plant has priorities for carbon allocation. The model

proposes that the parasite will access the host's carbon initially in terms of carbon intended for storage, next, in terms of carbon intended for growth, and finally, in terms of carbon allocated for respiration. If the model is accurate, then the presence of the parasite will initially be reflected in decreased amounts of stored carbon (i.e. starch), next, in decreased host growth (i.e. biomass allocation), and finally, by the death of the host.

To determine the accuracy of the proposed model, starch concentrations and several physical characteristics of uninfected and variously infected host trees were examined.

Physical characteristics which were altered as a result of dwarf mistletoe infection include needle number, mean needle length, needle biomass, mass per needle, total needle length and surface area, twig length, twig biomass, and twig unit mass. In general, the effect of the mistletoe was to decrease the annual allocation of carbon to infected tissues. This is what is predicted by the model.

The concentration of starch in infected tissues was found to be as much as 15 times that found in comparable uninfected tissues. This seems to be contradictory to the proposed model.

In terms of carbon budgets for branches, the proposed model was found to be inaccurate. Although the amount of carbon being allocated for biomass decreased, the concentration of starch in infected host tissues increased. However, in terms of the accuracy of the model for the entire tree, more work needs to be done. Work on whole tree biomass allocation has shown decreasing trends, however, no work has yet been done on entire tree starch concentrations.

THE EFFECT OF DWARF MISTLETOE (ARCEUTHOBIMUM AMERICANUM)
UPON A PORTION OF THE CARBON BUDGET OF LODGEPOLE PINE
(PINUS CONTORTA)

by

NANCY ELLEN BROSHOT

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE
in
BIOLOGY

Portland State University

1982

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INTRODUCTION

Parasitism is an exceedingly common means of existence. Price (1980) has estimated that over half of the animal species in the world are parasitic during a portion of their life cycles. This figure is much lower for plants. I estimate that approximately 3000 dicotyledonous species, or 1 to 2 % of all higher plant species, are parasitic. Although the number of species of parasitic plants is low, many of the species are ecologically important because of their common occurrence and wide distribution.

Frequently, ecologists treat parasitism as a type of predator-prey relationship (e.g. Crofton, 1971; Odum, 1971; Ricklefs, 1979; Anderson and May, 1978; Pianka, 1978; and Price, 1980). In both the parasite-host and the predator-prey associations, the interaction is beneficial to one member and detrimental to the other (Odum, 1959). However, I believe there are substantial ecological differences between the two types of associations. The predator's effect is to remove an individual from the prey population. An individual predator uses as its energy resource some part of its prey population over the course of its life span. On the other hand, parasites obtain nourishment from a single host over some period of time, often allowing the host to continue as an active member of its population. Parasites have as their energy resource, one individual host organism which sustains them until parasite reproduction occurs.

Throughout the time the host survives, its vigor and performance often decline as compared with uninfected individuals of similar age and type. This subtlety of decline may have very different effects on the community's structure and function than does the rapid removal of prey by predation.

Dwarf mistletoes (Arceuthobium) are a specialized group of vascular plant parasites which are parasitic primarily upon members of the family Pinaceae (figure 1). Arceuthobium is a member of the family Viscaceae and is represented in both the old and new worlds (Hawksworth and Wiens, 1972). As currently described, there are six old world species (Hawksworth and Wiens, 1972; 1976) and 32 new world species (Hawksworth and Wiens, 1972; 1977; and 1980). The greatest diversity occurs in northwest Mexico and the western United States and Canada. Seventeen of the new world species occur in the United States, of which, eight are found in Oregon (Hawksworth and Wiens, 1972; Knutson and Tinnin, 1981).

There is a range of host response to infection by Arceuthobium. Some of the host species show little response other than a local swelling of the twig at the site of infection. Other species show extensive modification of growth by the branch supporting the infection (Tinnin, Hawksworth and Knutson, 1982). I have selected for study from among the species readily available, a host-parasite complex which displays the widest range of host response.

When Arceuthobium americanum (Nutt. ex. Engelm.) infects its host (Pinus contorta var. murrayana (Dougl.)), there are two types of infections which may result. The first type is a local swelling

Figure 1. An example of a local swelling on Pinus contorta caused by Arceuthobium americanum.

(figure 1). In this type of infection, the endophytic system (the part of the Arceuthobium plant inside the host) is confined to that portion of the branch where the seed first landed. The host branch at this point becomes swollen, and the aerial shoots are confined to the swelling. The other type of infection is a systemic infection (figure 2). In this type of infection, the endophytic system of the parasite invades host buds and grows along with newly formed twigs. There is a loss of apical dominance which results in a proliferation of lateral shoots (Hawksworth and Wiens, 1972). In Pinus contorta, aerial shoots arise near bud scars on portions of twigs that are 3 to 10 years old.

The various species of Arceuthobium are relatively host specific (i.e. they grow predominantly on one host species). Arceuthobium americanum is found predominantly on Pinus contorta (lodgepole pine) and P. banksiana (jack pine), but it also occurs on P. ponderosa, P. aristata, P. albicaulis, P. flexilis, and is rarely found on Picea glauca, P. engelmannii, and P. pungens (Gill and Hawksworth, 1964; Hawksworth and Wiens, 1972). Arceuthobium americanum has the largest range of any of the North American dwarf mistletoes, occurring widely throughout the western United States and Canada (Hawksworth and Wiens, 1972). Throughout its range, A. americanum is responsible for heavy timber losses (e.g. Hawksworth and Lusher, 1956; Hawksworth, 1958a; Hawksworth and Graham, 1963; Gill and Hawksworth, 1964; Hawksworth and Hinds, 1964; Baranyay, 1970; Baranyay and Safranyik, 1970; Baranyay and Smith, 1972; Hawksworth and Wiens, 1972; Johnson, Hawksworth and Drummond, 1981). Studies have shown that from one-third to greater than one-half of all commercial, merchantable, lodgepole pine trees

are infected with this parasite (Hawksworth, 1958b; Gill and Hawksworth, 1964; Hawksworth and Hinds, 1964; Baranyay, 1970; Baranyay and Safranyik, 1970; Hawksworth and Wiens, 1972; Johnson, Hawksworth and Drummond, 1981). The amount of damage done is positively correlated with the length of time since infection and negatively correlated with the age of the stand when it became infected (Hawksworth, 1958; Hawksworth and Graham, 1963; Gill and Hawksworth, 1964; Hawksworth and Hinds, 1964). Reductions in growth (both in height and diameter) are reported to be 0.7 percent per year (Hawksworth and Hinds, 1964) with total reductions in growth of up to 31% in older trees (Baranyay and Smith, 1972).

Consequential reductions in volume occur with estimated merchantable volume losses at 270,750 cubic meters in Colorado and Wyoming national forests (Johnson, Hawksworth and Drummond, 1981) or 1.9 percent per year for stands in Colorado (Hawksworth and Hinds, 1964). As the infection becomes locally widespread throughout the canopy, mortality may result (Hawksworth and Lusher, 1956; Hawksworth, 1958; Andrews and Daniels, 1960; Gill and Hawksworth, 1964; Baranyay, 1970; Johnson, Hawksworth and Drummond, 1981). The mortality rate in severely infected stands may increase to as much as 5 times that of healthy stands (Hawksworth, 1958a). Often, the presence of the infection seems to predispose the host tree to a variety of other pathogens (e.g. fungi and insects) which kill the tree (Weir, 1916a; 1916b; Kuijt, 1960; Gill and Hawksworth, 1964; Baranyay and Smith, 1972; Hawksworth and Wiens, 1972). Just in the Colorado and Wyoming national forests, losses in potential income from timber sales due to A. americanum have been estimated at \$1.5 million per year (Johnson,

Figure 2. An example of a systemic "witch's broom" on Pinus contorta caused by A. americanum.

Hawksworth and Drummond, 1981).

The manner in which dwarf mistletoe reduces host growth is not known. It has been demonstrated that it is a strong sink on its host for water (Baranyay and Safranyik, 1970; Clark and Bonga, 1970; Mark and Reid, 1971; Fisher, 1975), minerals (McDowell, 1964), and carbon (Rediske and Shea, 1961; McDowell, 1964; Hull and Leonard, 1964a; 1964b; Leonard and Hull, 1965; Smith, et al, 1969; and Clark and Bonga, 1970). It has also been demonstrated to have the ability to alter its host's normal hormonal levels (Paquet, 1979). To what extent any or all of these factors play a role has yet to be determined. The goal of my research is to study the cause of decline among the hosts of A. americanum.

The carbon budget of the host

As the host plant photosynthesizes (figure 3), it fixes carbon, which is then utilized by the plant. Some of this carbon is irreversibly lost from the system through respiration, herbivory, or breakage. Some of the carbon is converted into structural components (i.e. cellulose) or secondary compounds (i.e. resin). Some of the carbon is converted into metabolic compounds (i.e. enzymes) and storage products (i.e. starch). While both of the latter components may be used by the plant, it is the storage component which is mobilized in times of carbon shortage. The addition of the parasite to the model adds a new dimension. It is not enough to know that the parasite is a carbon "sink". It is also important to know where and how the parasite alters its host's carbon budget.

The aerial shoots of Arceuthobium contain chlorophylls a and b

Figure 3. The carbon budget of the host tree.

(Hull and Leonard, 1964b), and are capable of photosynthesis. Miller and Tocher (1975) have shown that the aerial shoots of Arceuthobium tsugense are capable of supplying approximately 25 percent of their respiratory needs. The remainder must be made up by the host plant. Rediske and Shea (1961) demonstrated that translocation of photosynthate from the host to the parasite did occur. They also found a small amount of reverse flow (i.e. from the dwarf mistletoe, back to the host). They concluded that the mistletoe acts as a physical "girdle" to the host, preventing the boleward translocation of distally produced photosynthate beyond the point of infection. When Hull and Leonard (1964a; 1964b; and Leonard and Hull, 1965) repeated the experiments, they too came to the conclusion that the host supplies large quantities of photosynthate to the mistletoe, but they found no reverse flow, attributing Rediske and Shea's results to "leakage" in the experimental setup. Not only did Hull and Leonard find no translocation from the mistletoe back to the host, but they also found that there was no translocation from the aerial shoots back to the endophytic system of the dwarf mistletoe. They found no evidence of a physical barrier to translocation in the host, but that at certain times of the year, the mistletoe acted as such a strong sink, that little photosynthate remained available beyond the point of infection. Leonard and Hull also found that the presence of dwarf mistletoe could stimulate translocation from the main bole into defoliated, infected, lateral branches.

Since dwarf mistletoe is such a strong carbon sink, it seems reasonable to expect that any effect should be reflected in the most

mutable component of its host's carbon budget, storage. One of the primary storage products in pine is starch (Kozlowski and Keller, 1966; Kramer and Kozlowski, 1979; Webb, 1981). The effect that parasites have upon the starch content of their hosts has been examined for a variety of parasites (Allen, 1942; Inman, 1962; Singh, et al, 1968; Wardlaw, 1968; Smith, et al, 1969; Misra, 1970; MacDonald and Strobel, 1970; Daly, 1976; and DeLe Harpe, et al, 1981). Any type of parasitic infection generally leads to an increase in the starch concentration of the infected host tissues (Allen, 1942; Inman, 1962; MacDonald and Strobel, 1970; Daly, 1976). However, investigators working with parasitic vascular plants have found contradictory results. Singh, et al (1968), while finding an accumulation of starch in the tissues of Orobanche and Cuscuta, found that the infected host tissues generally contained less starch than uninfected controls. Misra (1970) found higher concentrations of starch in the host tissues that were infected with Dendrophthoe falcata. Munteanu and Kalo (1971) found higher concentrations of carbohydrates in host tissues infected with Viscum album. In Arceuthobium, Weir (1918) concluded that infected branches from witch's brooms contained higher amounts of starch than did uninfected branches. Hull and Leonard (1964a) found the opposite.

The proposed research

The specific aim of my study was to investigate the effect that Arceuthobium americanum has upon a part of the carbon budget of its host, Pinus contorta (lodgepole pine). As shown in figure 4, the host plant may be expected to have priorities for carbon allocation (Kramer and Kozlowski, 1979; Waring, et al, 1980). Assimilated carbon that

Figure 4. The effect of a parasite upon its host's carbon budget.

is in excess of the amount necessary to maintain metabolic functions can go for increases in structural biomass and finally for storage. The proposed model suggests that the parasite will initially access the host's carbon budget by way of its most available component, starch. Subsequent carbon removal would affect that allocated for growth, and finally, that allocated for respiration. If the model is accurate, the presence of the mistletoe should be reflected first, in a decreased amount of starch, then by decreased growth (i.e. biomass allocation), and finally, by decreased metabolic processes followed shortly thereafter by the death of the host tree. These effects will be directly related to the biomass of the parasite, although the amount of the parasite necessary to produce the effects is not known. The shape and slope of the function are also unknown.

My research investigated the storage and biomass allocation of the host and how it was altered with the addition of the parasite. Although the manner in which parasites alter the starch concentrations of their hosts has been reported (Weir, 1918; Hull and Leonard, 1964a; Singh, et al, 1968; Misra, 1970; Munteanu and Kalo, 1971; Daly, 1976), the results have been contradictory. Many workers have demonstrated decreases in both height and diameter growth in infected plants (Weir, 1916a; 1916b; 1918; Kuijt, 1960; Gill and Hawksworth, 1964; Hawksworth and Hinds 1964; Baranyay and Safranyik, 1970; Baranyay and Smith, 1972). There have also been indications of reductions in growth (both in needles and stems) of infected branches (Weir, 1916a; 1918; Kuijt, 1960). Recent work on Douglas fir (Tinnin and Knutson, 1980) has demonstrated branch and twig alterations caused by dwarf mistletoe such as reductions in twig mass per unit length, individual needle

mass, and increases in twig length.

I have tested the accuracy of my model by looking at concentrations of starch in uninfected and variously infected host tissues (both needles and twigs), and by measuring the following physical features of needles and twigs: needle number, needle length, needle biomass, total needle biomass, mass per needle, total needle surface area, twig length, twig biomass, and twig unit mass.

MATERIALS AND METHODS

Sites

Plant material was collected from two sites. Site 1 was located 13 miles south of Sisters, Oregon, on US Forest Service road 1534. This site was located at an elevation of approximately 2000 m. Site 2 was located on US Forest Service road 243-1, 1 mile off of highway 58. This intersection was 1.7 miles east of the Crescent Lake junction. This site was at an approximate elevation of 1750 m. Both sites were predominantly single species stands of Pinus contorta having mature trees of similar age, and growing on nearly level terrain.

At each site, the study area was divided into a 3x3 grid of one hectare squares. Three plots were than randomly selected from each grid. On each plot, all major canopy trees were numbered and rated according to the "6-point" dwarf mistletoe rating (DMR) system (Hawksworth and Lusher, 1956).¹ The trees were also placed in sub-categories according to whether the majority of infections present were of the local or the systemic type. Three trees from each sub-category in each available DMR class were then randomly selected.

1. In this system, the tree canopy is divided into three sections and each section is rated as: 0, uninfected; 1, lightly infected; or 3, heavily infected. The sum total of the values from the three sections is the DMR for that tree. A tree can thus be placed in categories ranging from 0 to 6, with 6 being a very heavily infected tree.

Other measurements were taken at the sites. At the time of twig collection, each tree was cored to determine its age, and height and DBH (diameter at breast height) were measured. At a later date, corings were again made to determine a 5 year radial growth increment. Also noted was bark thickness, overall needle color, needle longevity, and density.

Measurements of twig samples

Samples for chemical analysis were taken from branches that were located on the southwest sides of the trees. An attempt was made to collect all the samples from the same height on the trees (except in the case of the Sister's May 14, 1981 sample). As each sample was removed, the infection level was noted according to the following "branch rating" system (BRS): 0, uninfected branch from an uninfected tree; 1, uninfected branch from a infected tree; 2, one local swelling with no broom; 3, more than one local swelling with no broom; 4, non-systemic broom; 5, systemic broom; and 6, systemic broom with at least one local swelling. At the Crescent Lake site, samples were collected on June 22, 1980; November 15, 1980; and January 13, 1981. At the Sister's site, samples were collected on January 11, 1981 and May 14, 1981. The May 14th sample was collected in a different manner than the normal. An attempt was made to collect uninfected, local and systemic samples from each tree sampled. In doing so, samples were collected from several heights and compass orientations on each host tree.

All samples were labeled and placed in plastic bags which were

quickly placed on dry ice, transported back to the lab and placed in a freezer at -40° C.

Samples were removed from the freezer one at a time. Measurements of twig length, number of needles, and length of needles were made for the annual growth segments of 1978, 1979 and 1980 (figure 5). For the 1978 and 1980 categories, the needles and stems were separated and measured, and the fresh masses were determined to the nearest 0.1 mg. The samples were then placed in a drying oven at 80° C. for 48 hours and reweighed to determine dry mass. The 1979 growth increment was treated differently. As the needles were counted, one of each pair was set aside for further treatment. They were placed back in the freezer until they could be weighed and further prepared for chemical analysis. The other half of each fascicle was treated as a regular twig sample to obtain fresh and dry masses.

Preparation of starch samples

To determine the amount of starch in the tissue, the needles were ground in 10-20 ml of 0.5 N NaOH in a Sorvall Omni mixer at medium speed. Grinding time continued for five minutes after the last recognizable needle or stem segment was observed. The slurry was allowed to stand for 30 minutes, after which time it was neutralized with 0.5 N acetic acid.

To remove photometrically interfering compounds (i.e. pigments and phenolics) from the samples, enough Methanol:Chloroform:Water was added to the ground samples to bring the volumes to the desired ratio (M:C:W, 12:5:3 by volume). The samples were centrifuged, and the supernatant was removed and saved. The remaining residue was

Figure 5. Diagram of a systemically infected twig showing the annual growth segments.
(The bud scales have been exaggerated for reasons of clarification).

reextracted in a similar manner by adding M:C:W, 12:5:3, two to four times, until all pigments were removed and the resulting supernatant was clear. Polar compounds were separated from the pigments and lipids by adding 3 ml of glass distilled water per 5 ml M:C:W. Samples were mixed and allowed to stand several hours or overnight until the mixture separated. The pigmented lower layer (the chloroform layer) was removed and discarded and the upper, water-soluble layer was saved. The interface area between the two layers was centrifuged to ensure complete separation. The samples were placed in a 50° C. water bath overnight, under the hood, to drive off any remaining chloroform. One ml of 50% ethanol was added to the samples, which were then placed in a boiling water bath for 30 minutes to gelatinize the starch. After cooling, the samples were measured to the nearest ml, placed in glass bottles, and stored in the freezer (Haissig and Dickson, 1979).

Standard solutions

Starch: Approximately 4.5 mg of dried soluble starch was weighed accurately to the nearest 0.1 mg and dissolved in 2.5 ml of 0.5 N NaOH. This was stirred until all the starch was in solution, then diluted with distilled water to 20 ml. Acetic acid (0.5 N; 2.5 ml) was added and the solution diluted to a final volume of 45 ml. This solution served as a measured amount of starch used to calibrate the efficiency of the enzymes.

Enzymes: 10 mg of amyloglucosidase from Rhizopus (Sigma) was dissolved in 10 ml of sodium acetate buffer (0.1 M; pH=4.8). This solution was centrifuged before use (Dekker and Richard, 1971). In addition to amyloglucosidase, alpha amylase was added to ensure the

complete breakage of all starch chains (Webb and Karchesy, 1977).

Alpha amylase (type X-A; from Aspergillus oryzae) (0.5 g) was added to 30 ml of buffer (0.02 M sodium phosphate buffer; pH=6.9). This solution (0.5 ml) was added to 30 ml of the amyloglucosidase solution to give 10 units of amylase activity per ml of solution (Webb, pers. comm.).

A glucose oxidase solution was made by dissolving 30 mg of glucose oxidase (Sigma, type II, from Aspergillus niger), 10 mg of o-dianisidine hydrochloride (Sigma), and 3 mg of peroxidase (Sigma, from "horseradish") in 100 ml of tris-glycerol buffer (0.5 M; pH=7.0) (Dekker and Richards, 1971). This solution was stored at 4° C. in a brown glass bottle.

Chemical analysis of samples

Samples were divided into two aliquots; half were run with amylase to determine the total glucose content and half were run without amylase to determine the free glucose content. The amount of starch in the plant tissue was determined by the difference between free and total glucose.

To determine total glucose, 0.5 ml of the sample was mixed with 0.5 ml amyloglucosidase and alpha amylase solution, and placed in a 30° C. incubator for one hour. Two ml of glucose oxidase solution was then added, the solution was mixed and again placed in a 30° C. incubator for one hour. Four ml of 5 N HCl were added and the absorbance read in a Perkin-Elmer (model 124D) dual beam spectrophotometer at 540 nm.

To determine free glucose, one ml of sample was mixed with two ml

of glucose oxidase solution, and placed in a 30° C. incubator for one hour. Four ml of HCl were added, and the absorbance read.

A standard curve was run with each batch of samples. The standard curve consisted of known amounts of glucose from 0 to 54µg glucose/ml sodium acetate buffer.

Since fresh mass only was available for the ground samples, dry mass had to be estimated in order that the starch content could be expressed as µg starch per gram dry mass. Dry needle mass was estimated from the fascicle halves that were dried and weighed. The dry mass of the stems was estimated as the average of that from the years before and after the sample.

Statistical analysis

Statistical analyses were run on all the data. All data were compared to the dwarf mistletoe rating system (DMR), the branch rating system (BRS), and the infection class of the branch by means of a One-Way ANOVA and a linear regression with more than one value of y for each value of x. All the values were also subjected to a Student-Newman-Keuls test (Sokal and Rohlf, 1969; computer program by Withers).

RESULTS

Tables I and II show the mean DBH (diameter at breast height), height, age, annual radial increment, and 5 year radial growth increment for each DMR at each site. There was not an entire DMR range at either site. At the Crescent Lake site, the DMR ranged from 0 to 5, and at the Sisters site, the DMR ranged from 3 to 6. Thus, the entire DMR range could be examined only by reference to both sites. Because of the methods used to select sample trees, the data in Tables I and II are not characteristic for the stand as the whole, but are only representative of the trees selected for study.

A compilation of all data collected has been placed in the appendix. Not all trees were studied during each sampling date. The June 22 and the November 15 samples from the Crescent Lake site are incomplete due to mechanical failure. The Crescent Lake January 13 and the Sisters January 11 samples were randomly selected subsamples of the trees. Since different numbers of samples were taken from the trees, the number of samples in each DMR category varies. It is these two dates which will be extensively discussed in the text as they were most thoroughly sampled and all chemical procedures were well established.

As the Crescent Lake site was without systemic infections, several trees with systemic brooms were non-randomly selected from just outside the site.

TABLE 1

CRESCENT LAKE TREE CHARACTERISTICS

<u>DMR</u>	<u>DBH(cm)</u>	<u>HEIGHT(m)</u>	<u>AGE</u>	<u>MEAN ANNUAL INCREMENT (cm)</u>	<u>5 YEAR INCREMENT</u>	<u>N</u>
0	18.0	11.9	64	0.29	6.9	4
1	25.9	14.8	104	0.25	5.3	4
2	24.2	11.9	77	0.22	5.1	4
3	27.8	16.1	103	0.27	3.9	8
4	29.8	15.7	83	0.36	6.4	6
5	24.9	14.5	92	0.27	3.5	2

TABLE 11

SISTERS TREE CHARACTERISTICS

<u>DMR</u>	<u>DBH(cm)</u>	<u>HEIGHT(m)</u>	<u>AGE</u>	<u>MEAN ANNUAL INCREMENT(cm)</u>	<u>5 YEAR INCREMENT</u>	<u>N</u>
3	23.2	11.6	72	0.36 (9)*	6.1	10
4	24.1	12.5	72	0.35 (8)	6.6	11
5	26.3	13.4	85	0.32 (14)	5.3	16
6	25.0	13.3	93	0.27 (13)	4.5	19

*The number in parenthesis in the mean annual increment column is the number of samples that corings were available for. i.e. this is n for the age and annual increment columns.

Physical features vs DMR

Needle biomass (Table III) showed significant decreases as the dwarf mistletoe rating (DMR) increased. Results from the Student-Newman-Keuls (SNK) test showed this to be due to significant differences between uninfected and moderately to heavily infected trees. Mean needle number (Table III) exhibited a tendency to decrease as the DMR increased, but no significant difference was found. Mean needle length and mean mass per needle (Table III) were not significant with regard to DMR.

Length of twig segments (Table IV) did exhibit a significant relationship with DMR. Mean twig length tended to decrease, except with a DMR of 6, where an increase was found. SNK showed differences between uninfected and moderately infected trees, and moderately infected trees and trees with a DMR of 6. Twig biomass (Table IV) showed some tendencies for reduction in means with increasing DMR, but the relationship was, for the most part, insignificant. Twig unit mass (Table IV) showed no significant relationship with DMR.

Also examined was overall needle color, needle longevity, and needle density, bark thickness, and five year radial growth increment. Of these, only the radial growth increment (Table I, II) was found to be statistically significant ($p < 0.01$ for both sites), with means decreasing as the DMR increased.

Overall, DMR seemed to bear little relationship to any of the physical features of the tree. Needle mass, twig length, and radial growth increment were the only characteristics that were found to be significantly related to DMR, with needle biomass and radial growth

TABLE III

THE EFFECT OF DMR ON NEEDLE CHARACTERISTICS

CHARACTERISTIC	SITE	DMR						P
		0	1	2	3	4	5	6
NEEDLE NUMBER	CR	54(4) n=8	82(7) n=3	44(3) n=12	---	39(3) n=11	---	---
	S	---	---	---	61(6) n=18	60(7) n=16	43(6) n=17	46(7) n=14
<hr/>								
NEEDLE LENGTH(cm)	CR	3.1(0.3)	3.4(0.5)	3.4(0.2)	---	2.9(0.3)	---	---
	S	---	---	---	3.4(0.2)	3.1(0.2)	2.8(0.2)	2.9(0.2)
<hr/>								
NEEDLE BIOMASS(g)	CR	0.6479 (0.1026)	1.0118 (0.1676)	0.4361 (0.0838)	---	0.3890 (0.0875)	---	---
	S	---	---	---	0.8758 (0.1006)	0.5721 (0.1067)	0.4803 (0.1035)	0.5543 (0.1141)
<hr/>								
MASS PER NEEDLE(mg)	CR	11.9 (1.3)	11.8 (2.1)	10.9 (1.1)	---	9.2 (1.1)	---	---
	S	---	---	---	14.2 (1.2)	10.0 (1.2)	10.4 (1.2)	18.9 (1.3)

Each element is the mean for that DMR (standard error). n is the sample number which is listed once as it is the same throughout. P is the probability of significance as determined by a One-Way ANOVA.

TABLE IV

THE EFFECT OF DMR ON TWIG CHARACTERISTICS

<u>CHARACTERISTIC</u>	<u>SITE</u>	<u>DMR</u>						<u>P</u>
		0	1	2	3	4	5	6
TWIG LENGTH(cm)	CR	2.4(0.2) n=10	2.2(0.3) n=3	1.8(0.1) n=13	---	1.4(0.2) n=10	---	0.01
	S	---	---	---	2.5(0.3) n=18	2.6(0.3) n=17	2.0(0.3) n=17	2.1(0.3) n=13
TWIG BIOMASS(g)	CR	0.1783 (0.0195)	0.1398 (0.0355)	0.1112 (0.0171)	---	0.0901 (0.0195)	---	0.05
	S	---	---	---	0.2362 (0.0276)	0.1757 (0.0284)	0.1517 (0.0284)	0.1744 (0.0324)
TWIG UNIT MASS (mg)	CR	74.7 (5.8)	60.3 (10.7)	57.6 (5.1)	---	61.4 (5.8)	---	ns
	S	---	---	---	89.5 (7.1)	71.8 (7.3)	71.5 (7.3)	82.4 (8.3)

Each element is the mean for that DMR (standard error). n is the sample number and is listed once as it is the same throughout. P is the probability of significance as determined by a One-Way ANOVA. S is Sisters, Oregon; CR is Crescent Lake, Oregon.

decreasing as DMR increases, and twig length at first decreasing, and then increasing in trees with increasing DMR.

Physical features vs BRS (Infection class)

In an attempt to evaluate the mistletoe's localized effects on its host, the branch rating system (BRS) was devised. This method, rather than comparing the various growth characteristics to the infection level of the tree, instead compared the characteristics to the infection status of the branch from which they were collected. One interesting feature to emerge from this comparison, was the fact that the type of infection present seemed to have a greater impact on the host than the number of individual infections (i.e. one local infection had the same effect as did many). The branch rating system was, therefore, simplified to the infection class system and the same data was again analyzed. In this system, the samples were classified according to the infection status of the branch that they were taken from. There are three infection classes: 1) an uninfected branch; 2) a locally infected branch; and 3) a systemically infected branch.

Mean needle number (Tables V, VII) showed significant decreases as the branch rating increased. The number of needles was significantly less on locally infected branches. No apparent differences were found between systemic and nonsystemic branches. This result was observed at both sites.

Mean needle length (Tables V, VII) was significantly reduced at both sites as the branch rating increased. The differences were less definite between local and healthy branches, but needles from systemically infected branches were significantly shorter than from either

TABLE V

THE EFFECT OF BRANCH RATING ON NEEDLE CHARACTERISTICS

CHARACTERISTIC	SITE	BRANCH RATING							P
		0	1	2	3	4	5	6	
NEEDLE NUMBER	CR	54(5) n=8	65(6) n=5	43(3) n=17	30(10) n=2	40(10) n=2	---	---	0.05
	S	---	85(13) n=4	56(5) n=23	49(7) n=16	43(18) n=2	49(6) n=18	28(18) n=2	ns
NEEDLE LENGTH(cm)	CR	3.1 (0.2)	4.3 (0.3)	3.0 (0.2)	2.2 (0.5)	3.4 (0.5)	---	---	0.01
	S	---	4.1 (0.3)	3.5 (0.1)	3.3 (0.2)	4.2 (0.4)	2.0 (0.1)	2.7 (0.4)	0.001
NEEDLE BIOMASS(g)	CR	0.6479 (0.1026)	0.8705 (0.1297)	0.3959 (0.0704)	0.1964 (0.2051)	0.5359 (0.2051)	---	---	0.05
	S	---	1.5884 (0.1708)	0.7304 (0.0712)	0.6250 (0.0854)	0.6222 (0.2416)	0.3344 (0.0805)	0.2142 (0.2416)	0.001
MASS PER NEEDLE (mg)	CR	11.9 (1.0)	15.1 (1.2)	8.9 (0.7)	6.7 (2.0)	13.6 (2.0)	---	---	0.001
	S	---	20.2 (1.8)	13.2 (0.8)	12.6 (0.9)	14.4 (2.5)	6.4 (0.8)	7.7 (2.5)	0.001
TOTAL NEEDLE LENGTH (cm)	CR	165.5 (20.9)	272.7 (26.5)	129.8 (14.3)	66.0 (41.8)	135.6 (41.8)	---	---	0.001
	S	---	333.7 (43.7)	195.0 (18.2)	162.2 (21.9)	180.5 (61.9)	104.5 (20.6)	74.5 (61.9)	0.001
TOTAL NEEDLE SURFACE AREA (cm ²)	CR	606.1 (47.8)	834.1 (60.5)	580.2 (32.8)	439.2 (95.7)	672.5 (95.7)	---	---	0.01
	S	---	795.6 (59.4)	681.6 (24.8)	638.6 (29.7)	816.7 (84.0)	396.6 (28.0)	521.6 (84.0)	0.001

Each element is the mean for that branch rating (standard error). n is the sample number and is listed only once. P is the probability of significance as determined by a One-Way ANOVA.

TABLE VI

THE EFFECT OF BRANCH RATING ON TWIG CHARACTERISTICS

CHARACTERISTIC	SITE	BRANCH RATING						P	
		0	1	2	3	4	5		6
TWIG LENGTH(cm)	CR	2.4(0.1) n=10	2.4(0.2) n=6	1.6(0.1) n=16	1.1(0.3) n=2	1.5(0.3) n=2	-----	-----	0.001
	S	-----	3.6(0.6) n=4	2.0(0.3) n=13	1.8(0.3) n=16	2.7(0.8) n=21	2.8(0.5) n=18	1.8(0.8) n=2	0.05
TWIG BIOMASS(g)	CR	0.1783 (0.0166)	0.1756 (0.0214)	0.0935 (0.0131)	0.0462 (0.0370)	0.0625 (0.0370)	-----	-----	0.001
	S	-----	0.4260 (0.0517)	0.1708 (0.0220)	0.1612 (0.0258)	0.2844 (0.0731)	0.1655 (0.0237)	0.1664 (0.0731)	0.001
TWIG UNIT MASS(mg)	CR	74.7 (5.6)	70.3 (7.2)	58.0 (4.4)	53.4 (12.5)	43.4 (12.5)	-----	-----	ns
	S	-----	123.4 (12.5)	85.0 (5.3)	82.9 (6.2)	105.3 (17.6)	54.4 (5.7)	92.5 (17.6)	0.001

Each element is the mean for that branch rating (standard error). n is the sample number and is listed only once as it is the same throughout. S is Sisters, Oregon; CR is Crescent Lake, Oregon. P is the probability of significance as determined by a One-Way ANOVA.

healthy or locally infected branches.

Needle biomass (Tables V, VII) showed significant decreases as the branch rating increased. Needle biomass was significantly reduced by the presence of infection, and at the Sister's sites, showed significant reductions between systemically and locally infected branches.

Mass per needle (Tables V, VII) was significantly decreased with increasing infection level. In almost all cases, mass per needle decreased significantly from healthy to locally infected branches. In all cases with systemic samples, the systemic samples had significantly less mass per needle than did the non-systemic ones.

Total length of all the needles on the annual growth segment (Tables V, VII) was significantly reduced as the branch rating increased. This number decreased with increasing infection level.

Total surface area (as calculated from Mellor and Tregunna (1972)) (Tables V, VII) was significantly reduced as branch rating increased. As leaf surface area is commonly used as a measure of photosynthetic efficiency, the reductions here could be indicative of a corresponding decrease in the photosynthetic potential of the branch.

Twig length (Tables VI, VIII) was significantly reduced with increasing branch rating. Samples from locally infected branches were significantly shorter than those from healthy branches, while twigs from systemic brooms increased significantly in length over those from locally infected branches.

Even though twig length showed a decrease, followed by an

TABLE VII

INFECTION CLASS VS NEEDLE CHARACTERISTICS

CHARACTERISTIC	SITE	INFECTION CLASS			P
		1	2	3	
NEEDLE NUMBER	CR	58(4) n=13	42(3) n=21	---	0.01
	S	85(13) n=4	53(4) n=41	47(6) n=20	0.05
NEEDLE LENGTH(cm)	CR	3.5(0.2)	2.9(0.2)	---	0.05
	S	4.1(0.3)	3.4(0.1)	2.1(0.1)	0.001
NEEDLE BIOMASS(g)	CR	0.7335 (0.0807)	0.3904 (0.0635)	---	0.01
	S	1.5884 (0.1683)	0.6840 (0.0526)	0.3224 (0.0753)	0.001
MASS PER NEEDLE(mg)	CR	13.1(0.9)	9.1(0.7)	---	0.001
	S	20.2(1.8)	13.0(0.6)	6.5(0.8)	0.001
TOTAL NEEDLE LENGTH (cm)	CR	206.7(18.6)	124.2(14.7)	---	0.001
	S	333.7(43.2)	181.5(13.5)	101.5(19.3)	0.001
TOTAL NEEDLE SURFACE AREA (cm ²)	CR	693.8(42.4)	575.5(33.3)	---	0.05
	S	795.6(61.0)	671.4(19.0)	409.1(27.3)	0.001

Each element is the mean for that infection class (standard error). n is the sample number. P is the probability of significance as determined by a One-way ANOVA.

TABLE VIII

INFECTION CLASS VS TWIG CHARACTERISTICS

<u>CHARACTERISTIC</u>	<u>SITE</u>	<u>INFECTION CLASS</u>			<u>P</u>
		<u>1</u>	<u>2</u>	<u>3</u>	
TWIG LENGTH(cm)	CR	2.4(0.1) n=16	1.5(0.1) n=20	-----	0.001
	S	3.6(0.6) n=4	1.9(0.2) n=40	2.7(0.3) n=21	0.01
TWIG BIOMASS(g)	CR	0.1773 (0.0129)	0.0857 (0.0115)	-----	0.001
	S	0.4260 (0.0515)	0.1726 (0.0163)	0.1655 (0.0225)	0.001
TWIG UNIT MASS(mg)	CR	73.0(4.3)	56.1(3.9)	-----	0.01
	S	123.4(12.7)	85.2(4.0)	58.0(5.6)	0.001

Each element is the mean for that infection class (standard error). n is the sample number and is listed only once as it is the same throughout. S is Sisters, Oregon; CR is Crescent Lake, Oregon. P is the probability of significance as determined by a One-Way ANOVA.

increase, as infection class rose, twig biomass (Tables VI, VIII) was reduced with the presence of infection. And twig unit mass (Tables VI, VIII) was found to be significantly decreased among all three classes.

Infection class was found to be a highly significant method of predicting mistletoe's effect on its host's branches. Reductions were found in needle number, needle biomass, and twig biomass from uninfected to infected branches; needle length from healthy and local to systemic branches; and mass per needle, total needle length, total needle surface area, and twig unit mass from healthy to locally infected to systemically infected. Twig length decreased from healthy to locally infected twigs, and then increased in systemically infected twigs.

Starch concentration vs DMR and BRS (infection class).

The starch content of needles vs DMR (Table IX) was found to be significant in only one instance. In this case, it was shown by SNK as a matter of lightly infected vs moderately infected trees, but no clear trends emerged. Starch content of the twigs (Table IX) showed no significant differences in terms of DMR.

Needle starch content was significantly related to infection class (Table X) in all of the sample dates shown. In both cases, all classes were significantly different from the other classes, with the increasing infection classes (i.e. increasing infection level) causing increasing starch concentrations in the host tissues. The results from the Sister's May 14th sample were found to be not significant. However, this was the sample where there were increased variation in sampling techniques. Even so, the means show the same trends.

Twig starch content (Table X) was significant only at the

TABLE IX

DMR VS STARCH CONCENTRATION (% DRY MASS)

TISSUE TYPE	SITE	DMR						P
		0	1	2	3	4	5	6
NEEDLES	CR	1.25 (0.24) n=8	0.41 (0.39) n=3	1.36 (0.20) n=12	---	1.91 (0.20) n=11	---	---
	S	---	---	---	1.14 (0.64) n=18	1.33 (0.68) n=16	3.35 (0.66) n=17	1.75 (0.72) n=14
<hr/>								
TWIGS	CR	1.61 (0.82) n=10	1.40 (1.49) n=3	3.09 (0.72) n=13	---	3.77 (0.82) n=10	---	---
	S	---	---	---	1.92 (0.74) n=18	2.39 (0.76) n=17	3.41 (0.76) n=17	1.70 (0.87) n=13

Each element is the mean for that DMR (standard error). n is the sample number. S is Sisters, Oregon; CR is Crescent Lake, Oregon. P is the probability of significance as determined by a One-Way ANOVA.

TABLE X

INFECTION CLASS VS STARCH CONCENTRATION (% DRY MASS)

TISSUE TYPE	SITE	INFECTION CLASS			P
		1	2	3	
NEEDLES	CR	1.00(0.20) n=13	1.69(0.15) n=21	---	0.01
	S	0.24(1.28) n=4	1.21(0.40) n=41	3.63(0.57) n=20	0.05
<hr/>					
TWIGS	CR	1.30(0.58) n=16	3.87(0.52) n=20	---	0.01
	S	0.39(1.56) n=4	2.20(0.49) n=40	3.14(0.68) n=21	ns

Each element is mean for that infection class (standard error). n is the sample number.

S is Sister's Oregon; CR is Crescent Lake, Oregon. P is the probability of significance as determined by a One-Way ANOVA.

Crescent Lake site, where the locally infected branches had significantly more starch than the healthy branches. Nevertheless, the twig samples from the Sister's site showed the same increasing tendencies as the needle samples.

The effects that Arceuthobium americanum has upon the sampled characteristics of its host, Pinus contorta, are summarized in Table XI.

SUMMARY OF THE EFFECTS OF DWARF MISTLETOE UPON ITS HOST

<u>CHARACTERISTIC</u>	<u>SISTERS</u>	<u>CRESCENT LAKE</u>
Needle number	↓	↓
Needle length	↓	↓
Needle biomass	↓	↓
Mass per needle	↓	↓
Total needle length	↓	↓
Total needle surface area	↓	↓
Twig length	↓↑	↓↑
Twig biomass	↓	↓
Twig unit mass	↓	↓
Needle starch content	↑	↑
Twig starch content	ns	↑

Arrows refer to the effect of increasing infection class on the characteristic's mean. ↑ : means increase; ↓ : means decrease; ns: means are not significantly different as determined by a One-Way ANOVA.

DISCUSSION

Standard forestry techniques commonly use the dwarf mistletoe rating system (DMR) to categorize the infection level of the tree. Implicit in this is the implication that DMR is a useful indicator of the mistletoe's effect on its host. My data show agreement with the previously recorded decreases (Weir, 1916a; 1916b; Gill and Hawksworth, 1964; Hawksworth and Hinds, 1964; Baranyay and Safranyik, 1970; Baranyay and Smith, 1972) in radial growth (Tables I, II, IV) as the level of infection increases. This decrease in the annual allocation of carbon to wood volume is of primary concern to the timber industry. In this aspect, DMR seems to be a good indicator of how the parasite affects the lumber potential of its host. But, in terms of how the parasite alters the host physiologically, DMR seems to be a poor indicator. Besides radial growth, my results showed only needle biomass (Table III) and twig length (Table IV) to be significantly related to DMR and in both cases, it was uninfected vs heavily infected trees where the differences were apparent. These data suggest that DMR is not a very useful indicator of the mistletoe's effects on its host, except in cases of extremely infected trees.

The branch rating system (BRS) seemed to be a better method of estimating the localized effects of dwarf mistletoe upon its host than was DMR. Needle number, needle length, needle biomass, mass per needle, total needle length, total needle surface area (Tables V, VII),

twig biomass, and twig unit mass (Tables VI, VIII) were all significantly decreased as the level of the branch infection increased.

Dwarf mistletoe seems to affect the infected host branches in accord with the type of infection. The effects demonstrated by my data include: fewer needles on infected twigs (figure 6); smaller needles on infected twigs (figure 7), particularly in the case of systemic brooms; less massive needles on infected twigs (figure 8); and each needle having less mass as the infection level rises (figure 9). Calculated total length of all the needles for that year's annual growth segment (figure 10), as well as total surface area of those needles (figure 11), were both significantly reduced by infection. Although twig length (figure 12) showed an increase in the presence of systemic infection, the twigs showed a decrease in unit mass (figure 13) as the infection level rose.

The primary effect of dwarf mistletoe upon its host's physical features appears to be a reduction of carbon being allocated for biomass increases. This is in agreement with the proposed model (figure 4). These data also are in agreement with the known data (Weir, 1916a; 1916b; Gill and Hawksworth, 1964; Hawksworth and Hinds, 1964; Baranyay and Safranyik, 1970; Baranyay and Smith, 1972) on the subject. Tinnin and Knutson (1980) have demonstrated similar conditions in the systemically infected branches of Douglas fir. They too found reductions in twig unit mass and mass per needle, as well as an increase in twig length.

The biomass decrease, found in both needles and twigs, seems to be greater in systemically infected branches than in locally

Figure 6. The effect of infection upon needle number. Each point is the mean number of needles for that infection level with standard error indicated. ● is Sisters Oregon; ○ is Crescent Lake Oregon. U: uninfected; L: local swelling; S: systemic infection.

Figure 7. The effect of infection upon needle length. Each point is the mean needle length for each infection class with standard error indicated. ● is Sisters Oregon; ○ is Crescent Lake Oregon. U: uninfected; L: local swelling; S: systemic infection.

Figure 8. The effect of infection upon needle biomass. Each point is the mean total needle biomass for that twig segment for that infection class with standard error indicated. ● is Sisters Oregon; ○ is Crescent Lake Oregon. U: uninfected; L: local swelling; S: systemic infection.

Figure 9. The effect of infection upon mass per needle. Each point is the mean mass per needle with standard error indicated. ● is Sisters Oregon; ○ is Crescent Lake Oregon. U: uninfected; L: local swelling; S: systemic infection.

Figure 10. The effect of infection upon total needle length. Each point is the total needle length for each infection class with standard error indicated. ● is Sisters Oregon; ○ is Crescent Lake Oregon. U: uninfected; L: local swelling; S: systemic infection.

Figure 11. The effect of infection upon total needle surface area. Each point is the mean surface area for all the needles in that years segment for each infection class. Standard error is indicated. ● is Sisters Oregon; ○ is Crescent Lake Oregon. U: uninfected; L: local swelling; S: systemic infection.

Figure 12. The effect of infection upon twig length. Each point is the mean twig length with standard error indicated. ● is Sisters Oregon; ○ is Crescent Lake Oregon. U: uninfected; L: local swelling; S: systemic infection.

Figure 13. The effect of infection upon twig unit mass. Each point is the mean mass per unit length for each infection class with standard error indicated. • is Sisters Oregon; o is Crescent Lake Oregon. U: uninfected; L: local swelling; S: systemic infection.

infected branches. This suggests that the systemic type of infection may be more effective in controlling the carbon budget of the host, at least within a single branch.

My data also suggest that there may be a decrease in the photosynthetic efficiency of the host, as witnessed by the decreases in total needle length (figure 10) and total needle surface area (figure 11). But again, this represents losses to the branches, and not the tree.

While there seems to be a decrease in the amount of carbon being annually allocated to twig biomass, especially in systemic infections, it is necessary to keep in mind the unusual growth form of systemic brooms. Systemic brooms have many more actively growing shoots than do healthy branches. Tinnin and Knutson (1980) have reported that even small brooms may weigh 2.5 times more than comparable healthy host branches. As such, systemic brooms represent a significant rearrangement of host carbon, not necessarily a net loss of carbon.

The effect of the parasite on the host as a whole cannot be determined from my data. Recent work in our lab, however, has been conducted on biomass partitioning for the entire tree. Pairs of trees with near identical basal diameters, in close proximity to one another, were selected for comparison. One of each pair was heavily infected, and the other was as lightly infected as could be found. Analyses of the tree pairs reveal a tendency for net biomass and annual biomass allocation to be lower in heavily infected trees. There also seems to be a decrease in the ratio of needles to branches

in heavily infected trees so that they have a lower overall photosynthetic potential.

Starch

When DMR was utilized, no significant relationship with starch content was apparent. However, when either the branch rating system (BRS) or infection class were used, the starch content of the needles increased significantly as the level of the branch infection increased (figure 14). The starch content of the twigs did not show as strong a relationship as did the starch content of the needles, but the means still showed the same tendencies (figure 15). Starch concentrations for healthy twigs and needles averaged about 1% dry mass, whereas in infected tissues, means were 2% dry mass for locally infected tissues, and 3% dry mass for systemically infected tissues. However, the starch concentration of the local swellings themselves was never greater than 1% dry mass (n=5) with a mean of 0.1% dry mass.

The extremely low concentration of starch found in the infected tissue itself is in agreement with previously reported findings of Hull and Leonard (1964a), and makes sense in lieu of the fact that the mistletoe is such a strong carbon sink. The increase in starch content of the needles and twigs of that portion of the branch distal to the infection does not fit the model.

In reviewing the model of the parasite's effect on its host (figure 4), the assumption was that the first place the mistletoe would be drawing off of its host's carbon would be from the storage component (i.e. starch) and then from its structural component (i.e. biomass). On the basis of the observed tendencies of decreasing

Figure 14. The effect of infection upon the starch content of the needles. Each point is the mean starch concentration for each infection class with standard error indicated. ● is Sisters Oregon; ○ is Crescent Lake Oregon. U: uninfected; L: local swelling; S: systemic infection.

Figure 15. The effect of infection upon the starch content of the twigs. Each point is the mean starch concentration for each infection class with standard error indicated. ● is Sisters Oregon; ○ is Crescent Lake Oregon. U: uninfected; L: local swelling; S: systemic infection.

biomass both in branches and for the entire tree, it would appear that the mistletoe is indeed removing carbon from the structural pool. However, for the model to be correct, the mistletoe must be drawing a large amount of its carbon from the host's starch reserves. My data show the latter prediction to be invalid, within the organization of a single branch. It is possible, that in some manner, the mistletoe is altering the host branch so that it has an abnormally large starch reserve. This could be accomplished in a variety of ways: 1) by increasing the rate of photosynthesis in infected branches; 2) by decreasing the rate of respiration in infected branches; and 3) by altering the host's translocation rate, either into or out of the infected host branch. Work being conducted on the first two problems has revealed trends toward decreased respiratory rates in infected plants. Work on the third problem would best be accomplished through the use of labeled compounds.

The mistletoe also could be affecting the host plant so that the entire infected branch is acting as the sink, rather than just the parasite itself. This could be accomplished by altering the hormone concentrations of the infected host tissues, an already documented effect of Arceuthobium (Paquet, 1979). The dwarf mistletoe indirectly could be preventing or at least reducing the translocation rate out of the infected branch and into the rest of the plant. It also could in some manner prevent the plant from converting the excess carbon thus attained, into structural compounds. By maintaining the carbon in a more mutable form than that found in structural compounds, the starch would be readily available to the parasite.

CONCLUSION

It has long been recognized that Arceuthobium acts as a strong carbon sink upon its host (Rediske and Shea, 1961; Hull and Leonard, 1964a; 1964b; Leonard and Hull, 1965). The work presented here is a preliminary investigation into the physiological effects that dwarf mistletoe has upon the carbon budget of its host.

Physical features of the host which are altered as a result of mistletoe infection include needle number, mean needle length, needle biomass, mass per needle, total needle length and surface area, twig length, twig biomass, and twig unit mass. In general, the effect of the mistletoe is to decrease the annual allocation of carbon to the infected host tissues.

In contrast, the mistletoe's effect on the host's starch content is to increase it in infected tissue to as much as 15 times that in healthy branches. These two effects are seemingly contradictory. But while other studies have reported overall decreases in host growth, there is no knowledge of host starch content for the entire tree. Until this is known, the mistletoe's effect on the storage component will remain questionable.

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APPENDIX

LEGEND OF TABLES

ALL OF THE PROCEEDING TABLES CONTAIN THE FOLLOWING:

Each element is: mean $\pm$ standard error (sample error)

S: Sisters, Oregon

Cr: Crescent Lake, Oregon

P: is the probability of significance as determined by a One-Way ANOVA

*: significant value of r ($P < 0.05$) based on a linear regression for several values of y for each value of x

TABLE XII

DMR vs NEEDLE BIOMASS (G)

<u>SITE</u>	<u>DATE</u>	<u>DWARF MISTLETOE RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	1.3993±	0.8967±	0.7427±	0.7607±	0.6108±	0.2844±	
		0.2364 (3)	0.1832 (5)	0.2048 (4)	0.1548 (7)	0.2048 (4)	0.4093 (1)	
Cr	11/15	0.8222±	0.4560±	0.5089±	0.3319±	0.5752±		
		0.0829 (9)	0.0718 (12)	0.0718 (12)	0.1015 (6)	0.0786 (10)		ns
Cr	1/13	0.6479±	1.0118±	0.4361±		0.3890±		
		0.1026 (8)	0.1676 (3)	0.0838 (12)		0.0875 (11)		<0.01
S	1/11	---	---	---	0.8758±	0.5721±	0.4803±	
					0.1006 (18)	0.1067 (16)	0.1035 (17)	0.5543± 0.1141 (14)

DATA INCLUDE BIASED SAMPLES

Cr	1/13+s	0.6479±	1.0118±	0.4361±	0.2989±	0.3890±	0.2471±	
		0.1000 (8)	0.1633 (3)	0.0817 (12)	0.2000 (2)	0.0853 (11)	0.2000 (2)	<0.05
S	5/14	---	---	---	---	0.8643±	0.9175±	
						0.2146 (8)	0.1834 (13)	ns

TABLE XIII

DMR vs NUMBER OF NEEDLES

<u>SITE</u>	<u>DATE</u>	<u>DWARF MISTLETOE RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	73±9 (3)	55±7 (5)	43±8 (4)	59±6 (7)	47±8 (4)	53±15 (1)	---
Cr	11/15	65±5 (9)	47±4 (12)	48±4 (12)	42±6 (6)	48±5 (10)	---	ns
Cr	1/13	54±4 (8)	82±7 (3)	44±3 (12)	---	39±3 (10)	---	ns
S	1/11	---	---	---	61±6 (18)	60±7 (16)	43±6 (17)	46±7 (14)
								ns

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	54±4 (8)	82±7 (3)	44±3 (12)	61±8 (2)	39±3 (11)	49±8 (2)	---
S	5/14	---	---	---	---	61±10 (8)	54±8 (13)	---
								ns

TABLE XIV

DMR vs NEEDLE LENGTH (CM)

<u>SITE</u>	<u>DATE</u>	<u>DWARF MISTLETOE RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	4.0± 0.4 (3)	3.3± 0.3 (5)	2.5± 0.3 (4)	3.1± 0.3 (7)	3.2± 0.3 (4)	3.0± 0.7 (1)	---
Cr	11/15	3.3± 0.2 (9)	2.6± 0.2 (12)	3.1± 0.2 (12)	2.4± 0.2 (6)	3.0± 0.2 (10)	---	ns
Cr	1/13	3.1± 0.3 (8)	3.4± 0.5 (3)	3.4± 0.2 (12)	---	2.9± 0.3 (11)	---	<0.01
S	1/11	---	---	---	3.4± 0.2 (18)	3.1± 0.2 (16)	2.8± 0.2 (17)	2.9± 0.2 (14)

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	3.1± 0.3 (8)	3.4± 0.5 (3)	3.4± 0.2 (12)	1.5± 0.6 (2)	2.9± 0.2 (11)	1.9± 0.6 (2)	---	<0.05
S	5/14	---	---	---	---	3.2± 0.4 (8)	3.6± 0.3 (13)	---	ns

TABLE XV

DMR vs MASS PER NEEDLE (MG)

<u>SITE</u>	<u>DATE</u>	<u>DWARF MISTLETOE RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	18.9± 4.5 (3)	15.6± 3.5 (5)	19.1± 3.9 (4)	12.8± 2.9 (7)	12.5± 3.9 (4)	5.4± 7.7 (1)	---
Cr	11/15	12.3± 0.8 (9)	8.9± 0.7 (12)	10.4± 0.7 (12)	8.2± 1.0 (6)	11.8± 0.8 (10)	---	---
Cr	1/13	11.9± 1.3 (8)	11.8± 2.1 (3)	10.9± 1.1 (12)	---	9.2± 1.1 (11)	---	---
S	1/11	---	---	---	14.2± 1.2 (18)	10.0± 1.2 (16)	10.4± 1.2 (17)	18.9± 1.3 (14)
<hr/>								
DATA INCLUDES BIASED SAMPLES								
Cr	1/13+s	11.9± 1.2 (8)	11.8± 2.0 (3)	10.9± 1.0 (12)	4.7± 2.5 (2)	9.2± 1.1 (11)	5.0± 2.5 (2)	---
S	5/14	---	---	---	---	14.7± 3.3 (8)	20.0± 2.6 (13)	---

TABLE XVI

DMR vs TWIG LENGTH (CM)

DWARF MISTLETOE RATINGSITE DATE

	<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>P</u>
Cr 6/22	2.8± 0.4 (2)	2.3± 0.3 (3)	1.7± 0.5 (1)	1.7± 0.3 (4)	1.1± 0.4 (2)	---	---	<0.05
Cr 11/15	2.3± 0.2 (9)	2.0± 0.2 (11)	2.1± 0.2 (11)	1.6± 0.2 (6)	1.8± 0.2 (10)	---	---	ns
Cr 1/13	2.4± 0.2 (10)	2.2± 0.3 (3)	1.8± 0.1 (13)	---	1.4± 0.2 (10)	---	---	<0.01
S 1/11	---	---	---	2.5± 0.3 (18)	2.6± 0.3 (17)	2.0± 0.3 (17)	2.1± 0.3 (13)	ns

DATA INCLUDES BIASED SAMPLES

Cr 1/13+s	2.4± 0.2 (10)	2.2± 0.3 (3)	1.8± 0.2 (13)	5.2± 0.4 (2)	1.4± 0.2 (10)	2.8± 0.4 (2)	---	<0.001
S 5/14	---	---	---	---	2.9± 0.4 (8)	2.4± 0.3 (13)	---	ns

TABLE XVII

DMR vs TWIG BIOMASS (G)

SITE	DATE	DWARF MISTLETOE RATING						P
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	0.2544± 0.0458 (2)	0.1515± 0.0374 (3)	0.1051± 0.0647 (1)	0.1068± 0.0324 (4)	0.0705± 0.0458 (2)	---	---
Cr	11/15	0.1745± 0.0196 (9)	0.1415± 0.0181 (11)	0.1503± 0.0181 (11)	0.0906± 0.0244 (6)	0.1128± 0.0189 (10)	---	---
Cr	1/13	0.1783± 0.0195 (10)	0.1398± 0.0355 (3)	0.1112± 0.0171 (13)	---	0.0901± 0.0195 (10)	---	---
S	1/11	---	---	---	0.2362± 0.0276 (18)	0.1757± 0.0284 (17)	0.1517± 0.0284 (17)	0.1744± 0.0324 (13)

DATA INCLUDE BIASED SAMPLES								
Cr	1/13	0.1783± 0.0203 (10)	0.1398± 0.0371 (3)	0.1112± 0.0178 (13)	0.2235± 0.0454 (2)	0.0901± 0.0203 (10)	0.1306± 0.0454 (2)	---
S	5/14	---	---	---	---	0.2942± 0.0413 (8)	0.2319± 0.0324 (13)	---

TABLE XVIII

DMR vs TWIG UNIT MASS (MG)

<u>SITE</u>	<u>DATE</u>	<u>DWARF MISTLETOE RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	91.8±	63.9±	61.8±	60.4±	65.3±		
		11.5 (2)	9.4 (3)	16.2 (1)	8.1 (4)	11.5 (2)		
Cr	11/15	73.7±	72.1±	70.3±	54.9±	62.2±		
		6.9 (9)	6.3 (11)	6.3 (11)	8.5 (6)	6.6 (10)		ns
Cr	1/13	74.7±	60.3±	57.6±		61.4±		
		5.8 (10)	10.7 (3)	5.1 (13)		5.8 (10)		ns
S	1/11				89.5±	71.8±	71.5±	82.4±
					7.1 (10)	7.3 (17)	7.3 (17)	8.3 (13)

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	74.7±	60.3±	57.6±	41.8±	61.4±	46.3±	
		5.7 (10)	10.5 (3)	5.0 (13)	12.8 (2)	5.7 (10)	12.8 (2)	ns
S.	5/14					112.7±	100.9±	
						14.9 (8)	11.7 (13)	ns

TABLE XIX

DMR vs RADIAL INCREMENT

<u>SITE</u>	<u>DATE</u>	<u>DWARF MISTLETOE RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	7.6 $\pm$ 0.9 (3)	5.8 $\pm$ 0.9 (5)	6.0 $\pm$ 1.3 (4)	4.3 $\pm$ 0.7 (7)	4.3 $\pm$ 0.9 (4)	---	---
								ns
Cr	11/15	6.9 $\pm$ 0.5 (9)	5.9 $\pm$ 0.4 (12)	5.6 $\pm$ 0.5 (12)	4.3 $\pm$ 0.6 (6)	5.0 $\pm$ 0.4 (10)	---	---
								<0.01*
Cr	1/13	7.0 $\pm$ 0.4 (8)	6.0 $\pm$ 0.8 (3)	4.7 $\pm$ 0.4 (12)	---	4.2 $\pm$ 0.4 (11)	---	---
								<0.01
S	1/11	---	---	---	6.7 $\pm$ 0.6 (18)	4.6 $\pm$ 0.6 (16)	5.7 $\pm$ 0.6 (17)	4.1 $\pm$ 0.7 (14)
								<0.01

TABLE XX

BRANCH RATING vs NUMBER OF NEEDLES

<u>SITE</u>	<u>DATE</u>	<u>BRANCH RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	73±8 (3)	72±15 (1)	53±4 (14)	---	45±6 (6)	---	---
Cr	11/15	65±5 (9)	44±5 (8)	47±3 (28)	---	52±8 (4)	---	---
Cr	1/13	54±5 (8)	65±6 (5)	43±3 (17)	30±10 (2)	40±10 (2)	---	---
S	1/11	---	85±13 (4)	56±5 (23)	49±7 (16)	43±18 (2)	49±6 (18)	28±18 (2)
ns								

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	54±5 (8)	65±6 (5)	43±3 (17)	30±10 (2)	40±10 (2)	55±7 (4)	---
<0.05								
S	5/14	---	57±11 (6)	46±11 (6)	45±19 (2)	---	70±10 (7)	---
ns								

TABLE XXI

BRANCH RATING vs NEEDLE LENGTH (CM)

<u>SITE</u>	<u>DATE</u>	<u>BRANCH RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	4.0± 0.4 (3)	3.2± 0.7 (1)	3.1± 0.2 (14)	---	2.8± 0.3 (6)	---	---
Cr	11/15	3.3± 0.2 (9)	2.5± 0.2 (8)	2.9± 0.1 (28)	---	2.6± 0.3 (4)	---	---
Cr	1/13	3.1± 0.2 (8)	4.3± 0.3 (5)	3.0± 0.2 (17)	2.2± 0.5 (2)	3.4± 0.5 (2)	---	---
S	1/11	---	4.1± 0.3 (4)	3.5± 0.1 (23)	3.3± 0.2 (16)	4.2± 0.4 (2)	2.0± 0.1 (18)	2.7± 0.4 (2)
<hr/>								
DATA INCLUDES BIASED SAMPLES								
Cr	1/13+s	3.1± 0.2 (8)	4.3± 0.3 (5)	3.0± 0.2 (17)	2.2± 0.5 (2)	3.4± 0.5 (2)	1.7± 0.3 (4)	---
S	5/14	---	4.3± 0.2 (6)	4.2± 0.2 (6)	3.3± 0.4 (2)	---	2.1± 0.2 (7)	---

TABLE XXII

BRANCH RATING vs NEEDLE BIOMASS (G)

<u>SITE</u>	<u>DATE</u>	<u>BRANCH RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	1.3993±	1.0642±	0.7353±		0.6913±		
		0.2345 (3)	0.4062 (1)	0.1086 (14)	---	0.1658 (6)	---	---
Cr	11/15	0.8222±	0.3694±	0.5134±		0.4980±		
		0.0836 (9)	0.0887 (8)	0.0474 (28)	---	0.1254 (4)	---	---
Cr	1/13	0.6479±	0.8705±	0.3959±	0.1964±	0.5359±		
		0.1026 (8)	0.1297 (5)	0.0704 (17)	0.2051 (2)	0.2051 (2)	---	---
S	1/11	---	1.5884±	0.7304±	0.6250±	0.6222±	0.3344±	0.2142±
			0.1708 (4)	0.0712 (23)	0.0854 (16)	0.2416 (2)	0.0805 (18)	0.2416 (2)

DATA INCLUDE BIASED SAMPLES

Cr	1/13+s	0.6479±	0.8705±	0.3959±	0.1964±	0.5359±	0.2730±	
		0.0984 (8)	0.1244 (5)	0.0675 (17)	0.1967 (2)	0.1967 (2)	0.1391 (4)	---
S	5/14	---	1.3203±	0.9941±	0.5925±		0.5386±	
			0.2160 (6)	0.2169 (6)	0.3757 (2)	---	0.2008 (7)	---

TABLE XXIII

BRANCH RATING vs MASS PER NEEDLE (MG)

<u>SITE</u>	<u>DATE</u>	<u>BRANCH RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	18.9± 4.5 (3)	14.8± 7.9 (1)	13.2± 2.1 (14)	---	16.6± 3.2 (6)		
Cr	11/15	12.3± 0.9 (9)	8.5± 1.0 (8)	10.4± 0.5 (28)	---	9.7± 1.4 (4)	---	ns
Cr	1/13	11.9± 1.0 (8)	15.1± 1.2 (5)	8.9± 0.7 (17)	6.7± 2.0 (2)	13.6± 2.0 (2)	---	<0.05
S	1/11	---	20.2± 1.8 (4)	13.2± 0.8 (23)	12.6± 0.9 (16)	14.4± 2.5 (2)	6.4± 0.8 (18)	7.7± 2.5 (2)
								<0.001*

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	11.9± 0.9 (8)	15.1± 1.2 (5)	8.9± 0.7 (17)	6.7± 1.9 (2)	13.6± 1.9 (2)	4.8± 1.3 (4)	---	<0.001
S	5/14	---	25.4± 2.1 (6)	24.3± 2.1 (6)	13.1± 3.6 (2)	---	7.6± 1.9 (7)	---	0.001*

TABLE XXIV

BRANCH RATING vs TOTAL NEEDLE LENGTH (CM)

<u>SITE</u>	<u>DATE</u>	<u>BRANCH RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	295.7± 42.1 (3)	232.6± 73.0 (1)	170.9± 19.5 (14)	---	130.0± 29.8 (6)	---	---
Cr	11/15	223.3± 21.4 (9)	107.4± 22.7 (8)	142.5± 12.1 (28)	---	133.9± 32.1 (4)	---	<0.05
Cr	1/13	165.5± 20.9 (8)	272.7± 26.5 (5)	129.8± 14.3 (17)	66.0± 41.8 (2)	135.6± 41.8 (2)	---	<0.01
S	1/11	---	333.7± 43.7 (4)	195.0± 18.2 (23)	162.2± 21.9 (16)	180.5± 61.9 (4)	104.5± 20.6 (18)	74.5± 61.9 (2)
								<0.001
								<0.001

DATA INCLUDES BIASED SAMPLES

Cr	1/13 +s	165.5± 20.1 (8)	272.7± 25.5 (5)	129.8± 13.8 (17)	66.0± 40.3 (2)	135.6± 40.3 (2)	92.7± 28.5 (4)	---	<0.001
S	5/14	---	225.7± 40.0 (6)	179.8± 40.0 (6)	150.3± 68.5 (2)	---	149.4± 36.6 (7)	---	ns

TABLE XXV

BRANCH RATING vs TOTAL NEEDLE SURFACE AREA (CM²)[†]

SITE	DATE	BRANCH RATING						P
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	781.7± 75.3 (3)	633.3± 130.4 (1)	610.6± 34.9 (14)	---	541.8± 53.2 (6)	---	---
Cr	11/15	651.2± 36.7 (9)	487.7± 38.9 (8)	573.5± 20.8 (28)	---	507.4± 55.1 (4)	---	---
Cr	1/13	606.1± 47.8 (8)	834.1± 60.5 (5)	580.2± 32.8 (17)	439.2± 95.7 (2)	672.5± 95.7 (2)	---	---
S	1/11	---	795.6± 59.4 (4)	681.6± 24.8 (13)	638.6± 29.7 (16)	816.7± 84.0 (21)	396.6± 28.0 (18)	521.6± 84.0 (2)

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	606.1± 46.0 (8)	834.1± 58.2 (5)	580.2± 31.6 (17)	439.2± 92.0 (2)	672.5± 92.0 (2)	328.9± 65.1 (4)	---
S	5/14	---	834.3± 47.7 (6)	813.4± 47.7 (6)	648.0± 82.6 (2)	---	417.9± 44.1 (7)	---

[†] Surface area was calculated from Mellor and Tregunna (1972)

TABLE XXVI

BRANCH RATING vs TWIG LENGTH (CM)

<u>SITE</u>	<u>DATE</u>	<u>BRANCH RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	2.8± 0.3 (2)	3.1± 0.4 (1)	1.7± 0.2 (6)	1.3± 0.4 (1)	1.6± 0.3 (1)	---	---
Cr	11/15	2.3± 0.2 (9)	2.0± 0.2 (8)	1.9± 0.1 (26)	--	2.0± 0.3 (4)	---	---
Cr	1/13	2.4± 0.1 (10)	2.4± 0.2 (6)	1.6± 0.1 (16)	1.1± 0.3 (2)	1.5± 0.3 (2)	---	---
S	1/11	---	3.6± 0.6 (4)	2.0± 0.3 (13)	1.8± 0.3 (16)	2.7± 0.8 (21)	2.8± 0.3 (18)	1.8± 0.8 (2)
<hr/>								

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	2.4± 0.2 (10)	2.4± 0.3 (6)	1.6± 0.2 (16)	1.1± 0.4 (2)	1.5± 0.4 (2)	4.0± 0.3 (4)	---
S	5/14	---	2.4± 0.4 (6)	2.0± 0.4 (6)	2.1± 0.6 (2)	---	3.4± 0.3 (7)	---

TABLE XXVII

BRANCH RATING vs TWIG BIOMASS (G)

SITE	DATE	<u>BRANCH RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	0.2544± 0.0277 (2)	0.2628± 0.0392 (1)	0.1062± 0.0160 (6)	0.0758± 0.0392 (1)	0.0760± 0.0277 (2)	---	---
Cr	11/15	0.1745± 0.0203 (9)	0.1515± 0.0215 (8)	1.1268± 0.0119 (26)	---	0.0930± 0.0304 (4)	---	---
Cr	1/13	0.1783± 0.0166 (10)	0.1756± 0.0214 (6)	0.0935± 0.0131 (16)	0.0462± 0.0370 (2)	0.0626± 0.0370 (2)	---	---
S	1/11	---	0.4260± 0.0517 (4)	0.1708± 0.0220 (22)	0.1612± 0.0258 (16)	0.2844± 0.0731 (2)	0.1655± 0.0237 (19)	0.1664± 0.0731 (2)
<hr/>								
DATA INCLUDES BIASED SAMPLES								
Cr	1/13+s	0.1783± 0.0182 (10)	0.1756± 0.0235 (6)	0.0935± 0.0144 (16)	0.0462± 0.0407 (2)	0.0625± 0.0407 (2)	0.1771± 0.0288 (4)	---
S	5/14	---	0.3255± 0.0460 (6)	0.2716± 0.0460 (6)	0.1700± 0.0796 (2)	---	0.2066± 0.0426 (7)	---

TABLE XXVIII

BRANCH RATING vs TWIG UNIT MASS (MG)

<u>SITE</u>	<u>DATE</u>	<u>BRANCH RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	6/22	91.8± 8.6 (2)	84.8± 12.1 (1)	63.9± 4.9 (6)	58.3± 12.1 (1)	49.7± 8.6 (2)	---	---
Cr	11/15	73.7± 6.7 (9)	75.3± 7.1 (8)	66.3± 3.9 (26)	---	47.5± 10.1 (4)	---	---
Cr	1/13	74.7± 5.6 (10)	70.3± 7.2 (6)	58.0± 4.4 (16)	53.4± 12.5 (2)	43.4± 12.5	---	---
S	1/11	---	123.4± 12.5 (4)	85.0± 5.3 (22)	82.9± 6.2 (16)	105.3± 17.6 (2)	54.4± 5.7 (19)	92.5± 17.6 (2)
								<0.001

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	74.7± 5.4 (10)	70.3± 7.0 (6)	58.0± 4.3 (16)	53.4± 12.1 (2)	43.4± 12.1 (2)	44.1± 8.6 (4)	---	<0.05*
S	5/14	---	139.0± 9.0 (6)	131.8± 9.0 (6)	80.7± 15.6 (2)	---	61.0± 8.4 (7)	---	<0.001*

TABLE XXIX

INFECTION CLASS vs NUMBER OF NEEDLES

<u>SITE</u>	<u>CLASS</u>	<u>INFECTION CLASS</u>			<u>P</u>
		<u>1</u>	<u>2</u>	<u>3</u>	
Cr	6/22	73±7 (4)	51±3 (19)	---	<0.01
Cr	11/15	55±4 (17)	48±3 (32)	---	ns
Cr	1/13	58±4 (13)	42±3 (21)	---	<0.01
S	1/11	85±13 (4)	53±4 (41)	47±6 (20)	<0.05

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	58±4 (13)	42±3 (21)	55±7 (4)	<0.01
S	5/14	57±11 (6)	46±9 (8)	70±10 (7)	ns

TABLE XXX

INFECTION CLASS vs NEEDLE LENGTH (CM)

<u>SITE</u>	<u>DATE</u>	<u>INFECTION CLASS</u>			<u>P</u>
		<u>1</u>	<u>2</u>	<u>3</u>	
Cr	6/22	3.8±0.3 (4)	3.0±0.2 (19)	---	<0.05
Cr	11/15	2.9±0.2 (17)	2.9±0.1 (32)	---	ns
Cr	1/13	3.5±0.2 (13)	2.9±0.2 (21)	---	<0.05
S	1/11	4.1±0.3 (4)	3.4±0.1 (41)	2.1±0.1 (20)	<0.001

DATA INCLUDES BIASED SAMPLES

Cr	1/13	3.5±0.2 (13)	2.9±0.2 (21)	1.7±0.4 (4)	<0.001
S	5/14	4.3±0.3 (6)	3.9±0.2 (8)	2.1±0.2 (7)	<0.001

TABLE XXXI

INFECTION CLASS vs NEEDLE BIOMASS (G)

<u>SITE</u>	<u>DATE</u>	<u>INFECTION CLASS</u>			<u>P</u>
		<u>1</u>	<u>2</u>	<u>3</u>	
Cr	6/22	1.3156±0.2009 (4)	0.7239±0.0922 (19)	---	<0.01
Cr	11/15	0.6092±0.0680 (17)	0.5114±0.0496 (32)	---	ns
Cr	1/13	0.7335±0.0807 (13)	0.3902±0.0635 (21)	---	<0.01
S	1/11	1.5884±0.1683 (4)	0.6840±0.0526 (41)	0.3224±0.0753 (20)	<0.001

DATA INCLUDE BIASED SAMPLES

Cr	1/13+s	0.7335±0.0777 (13)	0.3902±0.0611 (21)	0.2730±0.1401 (4)	<0.01
S	5/14	1.3203±0.2160 (6)	0.8937±0.1871 (8)	0.5386±0.2000 (7)	<0.05*

TABLE XXXI I

INFECTION CLASS vs MASS PER NEEDLE (MG)

<u>SITE</u>	<u>DATE</u>	<u>INFECTION CLASS</u>			<u>P</u>
		<u>1</u>	<u>2</u>	<u>3</u>	
Cr	6/22	17.9±3.9 (4)	14.1±1.8 (19)	---	ns
Cr	11/15	10.6±0.7 (17)	10.3±0.5 (32)	---	ns
Cr	1/13	13.1±0.9 (13)	9.1±0.7 (21)	---	<0.001
S	1/11	20.2±1.8 (4)	13.0±0.6 (41)	6.5±0.8 (20)	<0.001*

DATA INCLUDES BIASED SAMPLES					
Cr	1/13+s	13.1±0.8 (13)	9.1±0.7 (21)	4.8±1.5 (4)	<0.001*
S	5/14	25.4±2.4 (6)	21.5±2.1 (8)	7.6±2.2 (7)	<0.001*

TABLE XXXIIII

INFECTION CLASS vs TOTAL NEEDLE LENGTH (CM)

<u>SITE</u>	<u>DATE</u>	<u>INFECTION CLASS</u>			<u>P</u>
		<u>1</u>	<u>2</u>	<u>3</u>	
Cr	6/22	279.9±37.2 (4)	158.7±17.1 (19)	---	<0.01
Cr	11/15	168.8±17.4 (17)	141.4±12.7 (32)	---	ns
Cr	1/13	206.7±18.6 (13)	124.2±14.7 (21)	---	<0.001
S	1/11	333.7±43.2 (4)	181.5±13.5 (41)	101.5±19.3 (20)	<0.001

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	206.7±18.0 (13)	124.2±14.1 (21)	92.7±32.4 (4)	<0.001
S	5/14	225.7±38.6 (6)	172.5±33.4 (8)	149.4±35.7 (7)	ns

TABLE XXXIV

INFECTION CLASS vs TOTAL NEEDLE SURFACE AREA (CM²)[†]

<u>SITE</u>	<u>DATE</u>	<u>INFECTION CLASS</u>			<u>P</u>
		<u>1</u>	<u>2</u>	<u>3</u>	
Cr	6/22	744.6±64.4 (4)	581.3±29.5 (19)	---	<0.05
Cr	11/15	574.3±29.1 (17)	565.2±21.2 (32)	---	ns
Cr	1/13	693.8±42.4 (13)	575.5±33.3 (21)	---	<0.05
S	1/11	795.6±61.0 (4)	671.4±19.0 (41)	409.1±27.3 (20)	<0.001

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	693.8±40.8 (13)	575.5±32.1 (21)	328.9±73.6 (4)	<0.001
S	5/14	834.3±50.3 (6)	772.1±43.5 (8)	417.9±46.5 (7)	<0.001

[†] Surface area was calculated from Mellor and Tregunna (1972)

TABLE XXXV

INFECTION CLASS vs TWIG LENGTH (CM)

<u>SITE</u>	<u>DATE</u>	<u>INFECTION CLASS</u>			<u>P</u>
		<u>1</u>	<u>2</u>	<u>3</u>	
Cr	6/22	2.9±0.2 (3)	1.6±0.1 (9)	---	<0.001
Cr	11/15	2.2±0.1 (17)	1.9±0.1 (30)	---	ns
Cr	1/13	2.4±0.1 (16)	1.5±0.1 (20)	---	<0.001
S	1/11	3.6±0.6 (4)	1.9±0.2 (40)	2.7±0.3 (21)	<0.01

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	2.4±0.2 (16)	1.5±0.1 (20)	4.0±0.3 (4)	<0.001
S	5/14	2.4±0.3 (6)	2.0±0.3 (8)	3.4±0.3 (7)	<0.05

TABLE XXXVI

INFECTION CLASS vs TWIG BIOMASS (G)

SITE	DATE	INFECTION CLASS			<u>P</u>
		<u>1</u>	<u>2</u>	<u>3</u>	
Cr	6/22	0.2572±0.0205 (3)	0.0961±0.0199 (9)	---	<0.001
Cr	11/15	0.1636±0.0147 (17)	0.1223±0.0111 (30)	---	<0.05
Cr	1/13	0.1773±0.0129 (16)	0.0857±0.0115 (20)	---	<0.001
S	1/11	0.4260±0.0515 (4)	0.1726±0.0163 (40)	0.1655±0.0225 (21)	<0.001

DATA INCLUDE BIASED SAMPLES

Cr	1/13+s	0.1773±0.0141 (16)	0.0857±0.0126 (20)	0.1771±0.0282 (4)	<0.001
S	5/14	0.3255±0.0463 (6)	0.2462±0.0401 (8)	0.2066±0.0428 (7)	ns

TABLE XXXVII

INFECTION CLASS VS TWIG UNIT MASS (MG)

<u>SITE</u>	<u>DATE</u>	<u>INFECTION CLASS</u>			<u>P</u>
		<u>1</u>	<u>2</u>	<u>3</u>	
Cr	6/22	89.5±6.7 (3)	60.1±3.9 (9)	---	<0.01
Cr	11/15	74.5±4.9 (17)	63.8±3.7 (30)	---	ns
Cr	1/13	73.0±4.3 (16)	56.1±3.9 (20)	---	<0.01
S	1/11	123.4±12.7 (4)	85.2±4.0 (40)	58.0±5.6 (21)	<0.001

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	73.0±4.2 (16)	56.1±3.8 (20)	44.1±8.4 (4)	<0.01
S	5/14	139.0±10.6 (6)	119.0±9.2 (8)	61.0±9.9 (7)	<0.001

TABLE XXXVIII

DMR vs STARCH CONTENT OF NEEDLES (% DRY MASS)

SITE	DATE	DWARF MISTLETOE RATING						P	
		0	1	2	3	4	5		6
Cr	1/13	1.25± 0.24 (8)	0.41± 0.39 (3)	1.36± 0.20 (12)	--- ---	1.91± 0.20 (11)	---	---	<0.01
S	1/11	---	---	---	1.14± 0.64 (18)	1.33± 0.68 (16)	3.35± 0.66 (17)	1.75± 0.72 (14)	ns

DATA INCLUDES BIASED SAMPLES									
Cr	1/13+s	1.25± 0.32 (8)	0.41± 0.53 (3)	1.36± 0.26 (12)	3.03± 0.65 (2)	1.91± 0.28 (11)	2.16± 0.65 (2)	---	<0.05
S	5/14	---	---	---	---	1.38± 0.29 (8)	1.36± 0.23 (13)	---	ns

TABLE XXXIX

DMR vs STARCH CONTENT OF TWIGS (% DRY MASS)

SITE	DATE	DWARF MISTLETOE RATING						P	
		0	1	2	3	4	5		6
Cr	1/13	1.61	1.40±	3.09±		3.77±			ns
		0.82 (10)	1.49 (3)	0.72 (13)	---	0.82 (10)	---	---	
S	1/11	---	---	---	1.92±	2.39±	3.41±	1.70±	ns
		---	---	---	0.74 (18)	0.76 (17)	0.76 (17)	0.87 (13)	

Cr	1/13	1.61±	1.40±	3.09±	1.95±	3.77±	2.99±		ns
		0.80	1.46 (3)	0.70 (13)	1.79 (2)	0.80 (10)	1.79 (2)	---	
S	5/14	---	---	---	---	1.38±	2.31±		ns
		---	---	---	---	0.39 (8)	0.30 (13)	---	

TABLE XXXX

BRANCH RATING vs STARCH CONTENT OF NEEDLES (% DRY MASS)

<u>SITE</u>	<u>DATE</u>	<u>BRANCH RATING</u>						<u>P</u>
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	1/13	1.25	0.60	1.64	2.63	1.21	---	---
		0.23 (8)	0.29 (5)	0.16 (17)	0.46 (2)	0.46 (2)	---	0.01
S	1/11	---	0.24	1.23	1.18	1.32	3.71	2.89
		---	1.31 (4)	0.55 (23)	0.66 (16)	1.86 (2)	0.62 (18)	1.86 (2)

0.05*

DATA INCLUDES BIASED SAMPLES

Cr	1/13+s	1.25	0.60	1.64	2.63	1.21	2.59	---	0.05
		0.32 (8)	0.40 (5)	0.22 (17)	0.64 (2)	0.64 (2)	0.45 (4)	---	
S	5/14	---	1.09	0.94	1.83	---	1.83	---	ns
		---	0.30 (6)	0.30 (6)	0.53 (2)	---	0.28 (7)	---	

TABLE XXXXI

BRANCH RATING vs STARCH CONTENT OF TWIGS (% DRY MASS)

SITE	DATE	BRANCH RATING						P
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>
Cr	1/13	1.61± 0.77 (10)	0.79± 0.99 (6)	3.73± 0.61 (16)	4.39± 1.71 (2)	4.42± 1.71 (2)	---	---
S	1/11	---	0.39± 1.58 (4)	2.14± 0.68 (22)	2.48± 0.79 (16)	0.53± 2.24 (2)	3.29± 0.73 (19)	1.70± 2.24 (2)
								<0.05
								ns

DATA INCLUDES BIASED SAMPLES

Cr	1/13	1.61± 0.74 (10)	0.79± 0.96 (6)	3.73± 0.59 (16)	4.39± 1.65 (2)	4.42± 1.65 (2)	2.47± 1.17 (4)	---	ns
S	5/14	---	1.40± 0.48 (6)	2.01± 0.48 (6)	1.78± 0.84 (2)	---	2.43± 0.45 (7)	---	ns

TABLE XXXXII

INFECTION CLASS vs STARCH CONTENT OF NEEDLES (% DRY MASS)

<u>SITE</u>	<u>DATE</u>	<u>INFECTION CLASS</u>			<u>P</u>
		<u>1</u>	<u>2</u>	<u>3</u>	
Cr	1/13	1.00±0.20 (13)	1.69±0.15 (21)	---	<0.01
S	1/11	0.24±1.28 (4)	1.21±0.40 (41)	3.63±0.57 (20)	<0.05

DATA INCLUDES BIASED SAMPLES					
Cr	1/13+s	1.00±0.25 (13)	1.69±0.20 (21)	2.59±0.46 (4)	<0.01
S	5/14	1.09±0.31 (6)	1.16±0.27 (8)	1.83±0.29 (7)	ns

TABLE XXXXIIII

INFECTION CLASS vs STARCH CONTENT OF TWIGS (% DRY MASS)

SITE	DATE	<u>INFECTION CLASS</u>			<u>P</u>
		<u>1</u>	<u>2</u>	<u>3</u>	
Cr	1/13	1.30±0.58 (16)	3.87±0.52 (20)	---	<0.01
S	1/11	0.39±1.56 (4)	2.20±0.49 (40)	3.14±0.68 (21)	ns

DATA INCLUDES BIASED SAMPLES					
Cr	11/13	1.30±0.57 (16)	3.87±0.51 (20)	2.47±1.13 (4)	<0.01
S	5/14	1.40±0.47 (6)	1.95±0.41 (8)	2.43±0.44 (7)	ns