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SHOOT GROWTH AND DEVELOPMENT OF DOUGLAS-FIR AND WHITE FIR IN NEW MEXICO[1]

J.-W. Briede, J. G. Mexal, A. M. Lynch and F. G. Hawksworth

ABSTRACT

Bud break and shoot growth of Douglas-fir (*Pseudotsuga menziesii*), with and without Douglas-fir dwarf mistletoe (*Arceuthobium douglasii*) infection, and white fir (*Abies concolor*) were evaluated over the 1988 and 1989 growing season. Crowns were partitioned into thirds for phenological measurements. Mistletoe infections were in the lower part of the crown. Timing of bud break was not influenced by crown position, although final shoot length was greatest in the upper crown, followed by middle crown, and the least elongation was in the lower parts of the canopy.

On Douglas-fir, more buds were present on non-infected trees than on broomed or non-broomed branches from infected trees. Infected branches showed a slightly accelerated bud initiation than all other branch types, although both infected and uninfected branches completed bud break within the same period. On infected trees, shoot elongation from brooms was greater than non-infected shoot growth from any part of the crown.

The implication for modeling of dwarf mistletoe and western spruce budworm (*Choristoneura occidentalis*) populations are discussed.

INTRODUCTION

Two major pests of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in southern New Mexico are western spruce budworm (*Choristoneura occidentalis* Freeman) and Douglas-fir dwarf mistletoe (*Arceuthobium douglasii* Engelmann). Detailed studies on both pests are available (Brookes *et al.* 1987; Tinnin *et al.* 1982; Hawksworth and Wiens 1972). Tinnin *et al.* (1982) conclude that mistletoe infections increase tree susceptibility to pathogens and decay organisms. Primary cause of increased susceptibility to other pests is weakening from changes in nutrient status. Death of mistletoe-infected trees always occurs after secondary pathogen and insect infestations (Hawksworth 1961; Tinnin *et al.* 1982); however, little is known about possible interactions among hosts and a combination of pests, including western spruce budworm.

In New Mexico, white fir (*Abies concolor* [Gord. & Glend.] Lindl.xHildebrande) is often associated with Douglas-fir. White fir is rarely infected by Douglas-fir dwarf mistletoe in New Mexico, and not at all by white fir dwarf mistletoe (*Arceuthobium abietinum* f. sp. *concoloris* (Hawksworth and Wiens 1972; Mathiasen and Hawksworth 1983). White fir is affected by spruce budworm, however. Data on the phenology and growth of these two tree species are important components in damage assessment and prediction through computer modeling.

The Prognosis-Western Spruce Budworm Modeling System is used by forest managers to predict western spruce budworm population dynamics and its effects on vegetation. It is also used to evaluate the effects of proposed treatments designed to mitigate the impact of budworm defoliation (Sheehan *et al.* 1987). The Prognosis Model projects tree stand growth and yield. The Budworm Dynamics Model includes foliage dynamics, insect population dynamics, weather, and insect dispersion components. The Budworm Damage Model includes foliage dynamics and tree damage models. This modeling system has been calibrated for several regions in western North America, but not for the southwestern United States. To adapt the existing models for use in New Mexico and Arizona, more information is needed on the phenological cycles of the host foliage.

This research examines seasonal changes in the phenology and morphology of Douglas-fir and white fir in southern New Mexico. In addition, the effects of Douglas-fir dwarf mistletoe on the growth and development of Douglas-fir are examined. Tinnin and Knutson (1980) provide some data on broom growth characteristics caused by *A. douglasii* in Oregon, by comparing branches of non-infected trees with twigs in brooms. However, they did not compare infected branches and non-infected branches on the same tree. Additionally, there are structural differences between brooms in New Mexico and brooms in central Oregon; brooms from New Mexico typically do not have the long pendant foliage shoots found in Oregon. The objective of this study was to provide data on foliage dynamics of both Douglas-fir and white fir as required by the Prognosis Model. Because mistletoe is an additional stress on the productivity of Douglas-fir and infected trees are susceptible to budworm attack, it was decided to study mistletoe-infected trees in more detail, examining both infected (broomed) and non-infected branches of the same tree.

METHODOLOGY

Four sites were selected in the Sacramento Mountains in the Lincoln National Forest (Figure 1). Three tree types were selected: Douglas-fir trees (1) with and (2) without mistletoe infestation, and (3) white fir. On mistletoe-infected trees, we sampled both infected and non-infected branches. At each site, we sampled approximately 15-25 trees for each tree type. Five trees per site were randomly selected for sub-sampling during each measurement period, which resulted in 10-15 trees being sampled on each date. Canopies were divided into crown thirds, and branches were collected from each layer. Crown position and height of the sampled branches were recorded. Sampling began the first week in May (1989) and continued on a weekly

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basis for the first month. Sampling was conducted every other week in June and July. Trees were sampled once in August. Measurements included current year's terminal bud diameter, flush length, needle length and number of lateral buds. In addition, flush length and needle length of the previous 5 years were recorded. Initially, the needle length for one randomly selected needle for each growth flush was measured. Subsequently, we measured one random needle in the current growth flush per twig. Data were analyzed as a completely randomized design with the PROC GLM procedure in SAS. Reported biological differences were significant at the $p<0.05$ level.

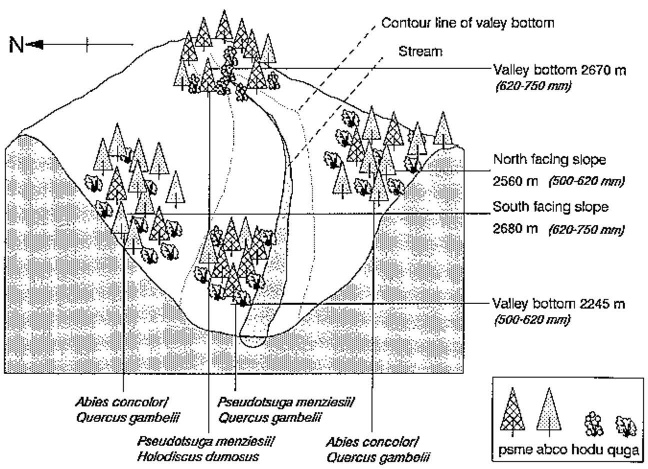

Figure 1.—Schematic overview of the study site. The location was in the Lincoln National Forest near Cloudcroft, NM (106° 25"W, 33° 18"N). Included are slope location, habitat type, precipitation and elevation.

RESULTS

Budbreak occurred over a 2-week period in 1989. Buds were swelling by April 18, but no elongation was evident. By April 27, more than 40% of the buds had initiated elongation. Virtually all buds were elongating by May 4. Douglas-fir exhibited the lowest rate of budbreak (18%) and branches from dwarf mistletoe brooms had the highest percentage (67%) on April 27, 1989 (Figure 2). Non-broom branches from infected trees were intermediate (38%). White fir branches had 50% of the buds elongating by this date. The small sample size (five trees) precluded statistical separation.

White fir completed flush extension approximately 2 weeks earlier than Douglas-fir (Figure 3). White fir completed most of its growth by the middle of June, while Douglas-fir exhibited growth until the beginning of July. Stem elongation in white fir was larger then Douglas-fir. Generally, in all observed trees, the top third of the canopy grew more than the middle third, which in turn grew more than the bottom (Figure 3). The top third of the canopy of white-fir grew 80 mm compared to 60 mm in uninfected Douglas-fir. The middle and bottom third of white fir grew approximately 55 mm, while Douglas-fir exhibited 35 and 30 mm growth for the middle and bottom, respectively.

White fir exhibited approximately twice the flush growth of Douglas-fir between 1984 and 1989 (Figure 4). During the past 5 years, canopies showed the same trends as in 1989, where the top third grew more than the middle, which grew more than the bottom third (Figure 4). Annual growth increments for non-infected Douglas-fir trees did not show specific relation with climate.

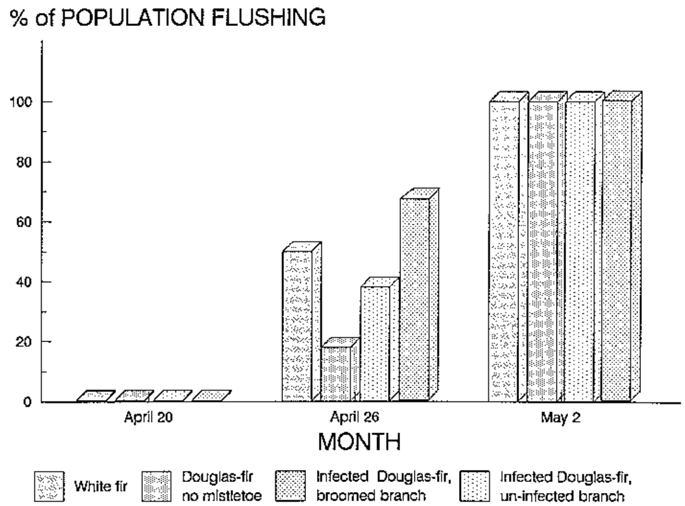

Figure 2.—Flush break dynamics for Douglas-fir and white fir during the spring of 1989.

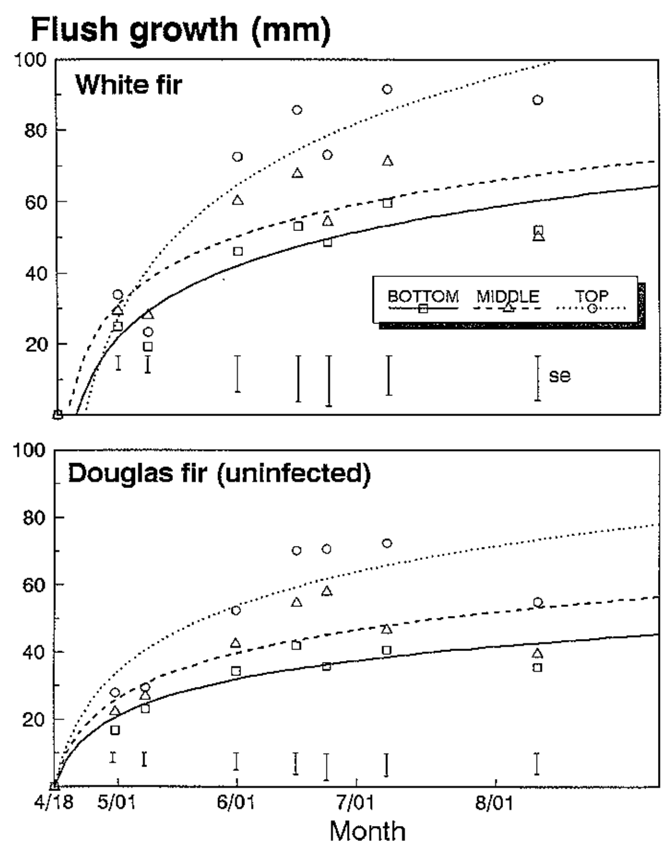

Figure 3.—Flush extension of white fir and non-infected Douglas fir during the 1989 growing season over canopy thirds. The bars indicate the standard error (se) for uninfected trees on a particular date.

Mistletoe infection altered the growth pattern of Douglas-fir (Figure 5). Growth of noninfected branches was greatly reduced in the upper crown compared to noninfected trees. Sample

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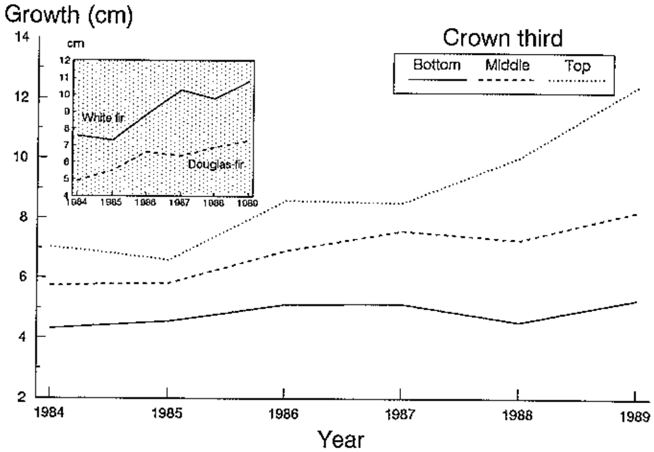

Figure 4.—Flush extension of non-infected Douglas-fir for 1984 through 1989 for the canopy thirds and a comparison between Douglas-fir and white fir (inset) for the whole canopy.

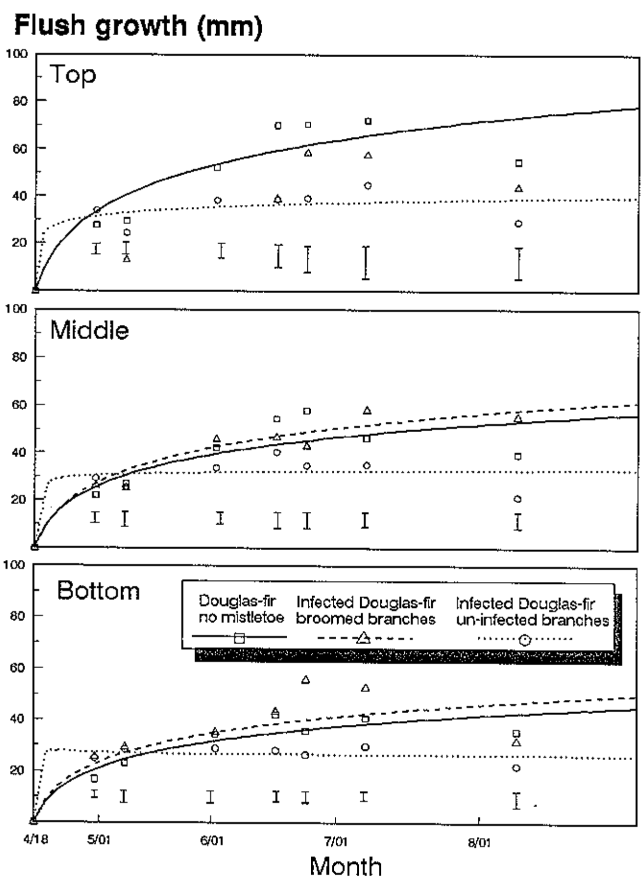

Figure 5.—Flush extension of the tree different Douglas-fir types for the three canopy thirds. The bars indicate the standard error (se) for uninfected trees on a particular date.

size was too small (n=2) to draw any conclusions regarding infected branches (in the top third of the canopy). In the lower two-thirds of the crown, there was no difference in elongation between branches of noninfected trees and broom branches of infected trees. However, non-broom branches of infected trees elongated little over the season. In fact, elongation was completed by May 17, 1989.

Non-infected trees produced significantly more buds than both branch types collected from infected trees (Table 1). Again, broomed branches are intermediate between non-infected branches on both infected and non-infected trees. On average, the top of the canopy had more buds than other layers, for all branch types. Differences in bud number between 1988 and 1989 may be the result of the heavy cone crop produced in 1988. No cones were produced in 1989.

Table 1.—Bud number for Douglas-fir trees at the end of the 1988 and 1989 growing season, divided over the canopy thirds.

Branch type	Top	Middle	Bottom
Non-infected (1989)	6.2^{b} B*	4.7^{b} A	3.0 A
Infected with broom (1989)	3.5^{ab}	2.6^{ab}	1.0
Infested without broom (1989)	2.8^{a}	1.7^{a}	1.3
Average 1989	4.2 B	3.0 B	1.8 A
Average 1988	2.6 B	2.1 AB	1.0 A

*Values followed by different lower case letters (a, b) are significantly different ($p<0.05$) within the same canopy third (vertical); values followed by different capitalized letters are significantly different ($p<0.05$) within the same row.

Little difference was detected between the needle lengths of the different branch types (Table 2). Non-infected trees seemed to have longer needles; however, only the data of the lowest canopy third were statistically different. White fir needles were approximately double the length of Douglas-fir needles (Table 2).

Table 2.—Differences in needle length between branch type and canopy third in Douglas-fir and white fir. The data is an average of needles, up until 5 years of age.

Branch type	Top	Middle	Bottom
Non-infected	20.1	19.4	19.6 B*
Infected with broom	18.7	18.8	18.2 A
Infected without broom	18.6	19.8	19.0 AB
White fir	36.3^{a}	39.7^{b}	38.8^{b}

*Values within the same column followed by different capitalized letters are significantly different; different lower case letters depict significant differences within the same row ($p<0.05$)

DISCUSSION

Brooms seen in infected Douglas-fir trees are a response to infections (Knutson 1983). These formations are characterized by a concentration of abnormal host twigs and foliage. Infection causes the rapid initiation and growth of adventitious buds, which in turn become infected with mistletoe. The cascading of this single, systemic infection causes the characteristic broom. Tinnin and Knutson (1980) report that infected Douglas-fir branches produce twice as many twigs, which in turn are 51-75% longer than twigs of branches from slightly-infected or non-infected trees. However, twigs from brooms have less biomass per unit length and more needles. The data from central Oregon (Tinnin and Knutson 1980) are quite different from

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the data reported in this paper, although Tinnin and Knutson did not compare infected and non-infected branches from heavily-infected trees. Comparing twigs from non-infected trees with twigs from brooms, our data indicates brooms had approximately the same amount of growth as non-infected trees. Comparing non-infected twigs on infected trees with twigs from brooms, we can see a growth depression between 28% and 80% on non-infected branches, which depends on the location in the crown third (top-middle-bottom had 28%, 81%, 79% depression, respectively). Non-infected branches on trees with brooms finished growth within 2 weeks, while the elongation of twigs in the brooms continued for approximately 8 weeks. The reduced flush extension might account for the differences in length, because the growth rate during the first 2 weeks appear to be similar.

All other measured parameters showed a similar response to mistletoe infection as seen with twig growth. Twigs from brooms showed a close resemblance to twigs from uninfected trees in needle length and bud number, while uninfected branches on infected trees showed the majority of the growth suppression. It appears that brooms are a sink for nutrients and water (Hull and Leonard 1964; Paquet 1978, 1979; Chen *et al.* 1978; Tocher *et al.* 1982; Fisher 1983; Knutson 1983; and Schaffer *et al.* 1983).

A physiological explanation for the altered sink source relationship is often considered to be the increase of the hormone cytokinin concentration at the site of infection. Paquet (1979) found Douglas-fir brooms had twice the amount of cytokinin compared to uninfected twigs. This increase in cytokinin may cause some of the morphological changes in brooms because cytokinins cause (1) changes in morphogenesis, (2) increased cell size, (3) delay of senescence and (4) increased pigment synthesis (Horgan 1984). These changes could be instrumental in the results seen by Tinnin and Knutson (1980), who report (1) larger twigs that were less dense per unit length and (2) more needles, but individual needle weight decreased. Both changes suggest either changes in cell size and/or morphogenesis. Because cytokinins are known to delay senescence, this may explain why brooms retain their needles approximately 2 years longer than non-infected trees (unpublished data).

Fisher (1983) concluded that mistletoe stems and fir needles on brooms may have less stomatal control than non-infected branches. This lack of stomatal control causes brooms to monopolize most of water taken up by the roots. Sustained growth of twigs infected by mistletoe is also controlled by cytokinin levels, which elicit the transport of nutrients towards the site of elevated concentrations (Horgan 1984). Nutrients are either retained in the broom, or brooms act as a resource sink, while the rest of the tree becomes the supplier of resources. This will result in the general growth depression seen in heavily infected trees (Tinnin *et al.* 1982).

Data presented here should help the various models that predict western spruce budworm outbreaks and damage. Indications are that most of the growth occurs in brooms of trees. Although it is not known where the carbohydrates which are fixed in the non-infected branches are translocated to, it seems that needle consumption by budworm of non-infected branches will be detrimental to the tree's survival. Uninfected branches seem to carry the maintenance of the trees, and carbohydrates fixed by brooms seem to be needed for maintenance and growth of the brooms and mistletoe.

Growth of non-infected branches in the upper crown is severely reduced in mistletoe infected trees. Western spruce budworm prefers to attack this upper crown portion, which causes an even larger reduction of photosynthetic area, resulting in top die-back and death of the tree. Furthermore, infected trees are more prone to diseases (Tinnin *et al.* 1982), which in combination with other pests, reduces productivity. It seems likely that increased stress from budworm attack results in high mortality rates of trees infected with dwarf mistletoe. However, rapid budbreak and completion of elongation may render the needles of infected trees unpalatable to emerging insects. Further study is warranted to determine if differences in phenology and growth of Douglas-fir, with or without mistletoe infection, creates an opportunity for preferential spruce budworm attacks.

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Authors

J. W. Briede
P & M Cole Co.
McKinley Mine
Gallup, NM 87305

J. G. Mexal
Department of Agronomy and Horticulture
Box 3Q
New Mexico State University
Las Cruces, NM 88003

A. M. Lynch
USDA Forest Service, Rocky Mountain Station
240 West Prospect
Fort Collins, CO 80526-2098

F. G. Hawksworth
USDA Forest Service, Rocky Mountain Station
240 West Prospect
Fort Collins, CO 80526-2098