INSECT DEFOLIATION STUDIES ON RED ALDER

(<u>ALNUS</u> <u>RUBRA</u> BONG.) ON BURNABY

MOUNTAIN, B.C.

by

Peter Muthigani

B.Sc., University of East Africa, 1967

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE

REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biological Sciences

Simon Fraser University

August, 1971

APPROVAL

Name: Peter Muthigani

Degree: Master of Science

Title of Thesis: Insect defoliation studies on Red Alder
(<u>Alnus</u> <u>rubra</u> Bong.) on Burnaby Mountain,
B.C.

Examining Committee:

Chairman: G.H. Geen

A.L. Turnbull
Senior Supervisor

B.P. Beirne

J.H. Borden

R.C. Brooke

G.R. Lister

Date Approved: *26 Oct 1971*

ii

ABSTRACT

Defoliation of <u>Alnus</u> <u>rubra</u> Bong. saplings on Burnaby

Mountain, B.C., between August 1970 and August 1971 was mainly

caused by two chyrsomelid beetles, <u>Pyrrhalta</u> <u>punctipennis</u>

(Mannerheim) and <u>Altica</u> <u>ambiens</u> Le Conte and one sawfly,

<u>Eriocampa</u> <u>ovata</u> L. (Hymenoptera, Tenthredinidae). Insect

damage was low until August. Between mid-June and the autumn

there was a progressive decline in the numbers of leaves per

tree. The number of leaves damaged increased steadily from

June on, but the proportion of each leaf damaged remained

small until mid-August. After mid-August the damage per leaf

increased rapidly, and by early September severe leaf damage

was apparent. No relationship was established between leaf

surface lost to defoliators and stem wood volume increment or

between residual leaf surface in the autumn and stem growth.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

INTRODUCTION

Little work has been done on methods of measuring damage
to either forest or agricultural crops by defoliating insects
(Strickland et al., 1970). Judging by the scarcity of reviews
and papers, the manner in which defoliation influences the
growth of crop plants and forest trees has not been studied
adequately (Kulman, 1971). One result of this deficiency is
that it is difficult to assess objectively the need for con-
trol measures. Conspicuous but superficial damage may elicit
excessive and uneconomical controls while cryptic but signifi-
cant damage may go untreated. Economic injury levels of pest
density must be determined carefully; there are factors that
influence the market value of the crop that must be considered
entirely apart from total productivity (Stern et al., 1959).
Crop loss assessments must be devised before pest control
costs and the market value of the crop can be superimposed
(Stern et al., 1959).

This thesis attempts to assess the effects of defoliating
insects on the productivity and growth of red alder (<u>Alnus
rubra</u> Bong.)

<u>ALNUS RUBRA BONG</u>.

Red alder is the most abundant hardwood in the Pacific

Northwest and coastal Alaska. The total red alder volume was estimated in 1957 to be about 12.5 billion board-feet, about 90% of which was in Washington and Oregon (Worthington, 1957). The volume of red alder is only about 3% of the conifer volume in the Pacific Northwest. In Washington and Oregon, increasing amounts of red alder are being used for pulpwood and lumber (Worthington, 1957). Red alder is generally relegated to the status of a weed tree in conifer forests, on roadsides and along power lines, among other locations. It is probable that it will be regarded as an economically important tree in the future.

I. Taxonomy

Alnus rubra Bong. (= Alnus oregona Nuttal)(Betulaceae) is the largest species in the genus Alnus. It is also known as Pacific Coast alder, Oregon alder and Western alder. Alnus rubra Bong. is the name accepted by Johnson (1968).

The form of the tree and leaf morphology distinguish it easily from other Alnus species. There is a single bole which is smooth and tapering and the crown is short and dome-shaped. The leaves have a serrated margin with a characteristic inroll.

II. Range

Red alder occurs in the Pacific Coast region from south-east Alaska to Southern California, latitudes 60°N and 34°N

respectively. It generally occurs below an elevation of 2500 feet and less than 100 miles from the ocean (Worthington et al., 1962). It is prevalent along river valleys, lowlands and moist mountain slopes. Fig. I shows the range of A. rubra.

III. Salient features of A. rubra ecology and life history

Red alder is an important component in three cover types in the Pacific Northwest; the red alder type, the Sitka spruce type and the Sitka spruce-western hemlock type. It also occurs in clumps in the Douglas-fir type, the Douglas-fir - western hemlock type and the western red cedar type. It is thus widespread in coniferous forest communities (Worthington et al., 1962).

A. rubra has exacting moisture requirements, 25 inches of precipitation per annum or more being necessary. The annual precipitation over most of its range varies from 25-120 inches. It generally thrives on all slopes at low elevations but north and east-facing slopes are favoured where precipitation is low.

Red alder propagates itself by means of small wingless seeds, called nutlets, which are born in hard black cones. Seed production begins at about 10 years of age and continues to maturity; alder has a longevity of 50-70 years. The seeds are produced in very large quantities. Dispersal of seeds is

Fig. I. The range of red alder

by wind. The seeds must have full overhead light for germina-
tion. Young seedlings can tolerate shade for the first two
years but thereafter they must have full overhead light. The
requirement for full overhead light explains why red alder is
a pioneer species in areas where existing vegetation has been
cleared by logging and where areas have been denuded by fire
or ice storms. Red alder seedlings grow very rapidly after
the first year; where conifers of the same age are present
red alder outstrips them in height growth, overshades them,
and inhibits their growth. This characteristic makes red alder
a major weed species in conifer forests. Red alder is over-
taken by conifers after about 20-30 years of growth. But in
extra moist soils of high organic content, such as valley bot-
tom soils, alder maintains its dominance and becomes the climax
vegetation (Worthington et al., 1962).

IV. Red alder and nitrogen fixation

The genus *Alnus* is one of the few genera of Angiosperm
plants that can fix atmospheric nitrogen. This important
physiological process was first demonstrated in European alder,
Alnus glutinosa (L.) (Bond, 1956). Most *Alnus* spp. including
A. rubra carry the root nodule endophyte responsible for the
assimilation of free nitrogen.

Tarrant (1963) considers that red alder foliage is per-
haps more important than root nodules as the direct source of
nitrogen compounds available for recycling.

During a 26 year period, A. rubra was estimated to add 36
pounds of fixed nitrogen per acre per annum (Tarrant, 1963).
The mean annual accumulation rate for fixed nitrogen in mixed
plantings with Douglas-fir was 56.6 lbs./acre. In Alaska,
studies on a recently deglaciated area where Sitka alder,
Alnus sinuata (Regel) Rydberg, was becoming established had
a mean annual accumulation rate of 55 lbs. per acre (Crocker
and Major, 1955).

Tarrant et al (1968) found that fixed nitrogen and organic
matter content increased in mixed plantings of A. rubra and con-
ifers. Yamaya (1968) reported that the rate of nutrient cycling
under alder forests is very rapid. Thus, although alder in-
creases organic matter and nitrogen content, the trees would
have to be cut to break the cycle and to release the extra
nutrients in the soil for use by other tree species.

The nitrogen fixation capacity of alder, its rapid growth
and the rapid cycling of nutrients in alder forests have been
exploited in various ways:-

a) In Europe alder has been used to stabilize flood de-
posits and landslide areas and to reclaim mine spoils.

b) Although still only potentially important, the use
of alder for improving the growth of associated timber species,
or in rotation with species, is probably the most interesting.
The following tree genera have been found to do better in the
presence of alder than its absence (Tarrant et al, 1968): _Fraxinus_,
Liquidambar, _Liriodendron_, _Picea_, _Pinus_, _Platanus_, _Populus_ and
Pseudotsuga. This is probably due to the capacity of alder
species to enhance soil fertility.

V. _Growth and Yield_

_A_. _rubra_ is the largest of the six species of alder in
North America. Maximum diameter ranges from 24-30" while max-
imum height is 100-130 ft. Generally, red alder has a long
pencil-like bole and hence is suitable for lumber. The trees
with very large diameters tend to have short merchantable boles
and are less suitable for lumber.

Red alder grows largely in mixed forests. This scattered
distribution makes measurement of volume increments per unit
area difficult. The mean annual increment varies widely de-
pending on the density and distribution of alder and on the
site characteristics of the chosen area. As one would expect,
pure stands, low in acreage, have higher mean annual increments;
they tend to be found in areas of optimum moisture and soil

conditions such as valley bottoms containing alluvial soils. Pure stands, on the average, have mean annual yields of about 400-500 board feet per acre. This is about 20,000 to 35,000 bd. feet per acre on a 50-70 year rotation (Worthington, 1957).

Average yields for red alder are less than conifer yields. This is due to:-

a) The shorter merchantable tree height of red alder. Merchantable height of red alder at 50 years of age is 40-50 feet while the comparable height for conifers associated with alder is 65-90 feet.

b) The larger crown area per acre of red alder, and therefore, fewer stems per acre. This is true only of mature alder. Young alder, below 15 years of age, often attains such a high density that there is virtually no understorey vegetation.

Removal of virgin conifer forests through logging etc., tends to favour encroachment by red alder. Hence, the total volume of red alder, although only about 3% of the softwood volume in the Pacific northwest, may increase as more conifer forests are denuded.

Examples of yield tables for red alder are shown (Table 1).

-9-

TABLE 1. Examples of yield tables for red alder

PACIFIC NORTHWEST YIELD TABLES[1]

Age (years)	Board-foot yield[2]		Cubic-foot yield[3]	
	Average net volume	Mean annual increment	Average net volume	Mean annual increment
10			120	12
20	100	5	1,620	81
30	6,800	227	2,930	98
40	13,700	342	4,030	101
50	20,600	412	4,940	99
60	27,300	455	5,640	94
70	33,800	483	6,150	88

BRITISH COLUMBIA F.S. YIELD TABLES[4]

Age (years)	Average net volume	Mean annual increment	Average net volume	Mean annual increment
10			1,520	152
20	3,400	170	2,850	142
30	12,750	425	3,950	132
40	23,500	588	4,675	117
50	30,750	615	5,200	104
60	35,000	583	5,600	93

1. Site index is 90 feet (50 years).

2. PNW table: Scribner rule for all trees larger than 9.5 inches d.b.h. to a fixed top diameter of 8 inches (inside bark). Scaled in 8-foot logs.
B.C. table: B.C. rule for all trees larger than 6.5 inches d.b.h. to an average top diameter of 8 inches (outside bark). Scaled in 8-foot sections.

3. PNW table: All trees larger than 5.5 inches d.b.h. to a minimum 4-inch top (inside bark).
B.C. table: All trees larger than 0.9 inch d.b.h.

4. British Columbia Forest Service (1947). Site index is 96 feet (50 years).

From Worthington et al 1962. Red alder, its management and utilization. U.S. Dept. Agr. Misc. Pub. 881.

VI. <u>Characteristics as a tree and a wood; present uses; potential uses</u>

Most of the Pacific coast red alder is in Washington and Oregon and most of the commercial uses of alder referred to below apply to these areas. Elsewhere, red alder is only of minor use and is treated as a weed species, especially where it encroaches on land suitable for conifers. Thus, in British Columbia, it is generally regarded as brush, alongside broadleaf maple (<u>Acer</u> <u>macrophyllum</u> Pursh), vine maple (<u>Acer</u> <u>circinatum</u> Pursh), <u>salmonberry</u> (<u>Rubus</u> <u>spectabilis</u> Pursh), bracken (<u>Pteridium</u> <u>aquilinum</u> L) and salal (<u>Gaultheria</u> <u>shallon</u> Pursh).

In British Columbia, alder is estimated to occupy 105,000 acres (Hetherington, 1964). In B.C. alder is the main target of brush control. Control measures against brush are used prior to planting conifers in locations where alder is already established; where alder invades a conifer plantation it assumes the status of a major weed species and control is required.

Prior to World War II, red alder was relatively untapped as a commercial tree. Since then, it is regarded as a potentially valuable timber species. Within the last decade it has assumed value as a pulpwood source. This change in its economic status is attributed to various factors, e.g.:-

a) Decline in quality and quantity of traditional hardwood

sources has served to focus attention on the good qualities

of red alder as a wood. It was long recognized as a suitable

wood for furniture but was overshadowed by other hardwoods.

b) Technological advances in alder pulping have made it

a potentially valuable species for fine tissues.

c) The economics of managing and utilizing red alder are

not adequately researched, so far. But it is apparent that

most of the alder acreage is in the coastal belt and is readily

accessible.

The alder tree is straight and clear boled for 50-60% of

its height when grown in relatively dense stands. Limbs are

shed rapidly. In early growth, it tends to grow straight up

towards the overhead light; hence the pencil-like form. Its

bark is thin.

The wood is whitish when freshly cut but turns brown quick-

ly due to oxidative reactions. Red alder wood has a fine even

texture and straight grains. Growth rings show clearly.

The following properties of alder make it a useful furni-

ture wood; it is moderately hard, it machines well, it takes

finish well, it is easily glued, it does not split readily

on nailing, and when seasoned, it does not shrink or warp

appreciably.

In addition to common furniture manufacture, it is used

as core stock and cross bands in plywood.

Pulpwood exceeds furniture as the main use for red alder in Washington and Oregon. This is a fairly recent development. Red alder grows very rapidly and has a short generation time from establishment to harvest. It has a thin bark and straight clean bole which are good features for a pulpwood; there is little wastage and the material to be pulped is fairly homogeneous. It is suitable for the following products:-

i) Sulphite alder pulp is blended with softwood pulp to make high-grade tissue. Red alder has short, soft cellulose fibers which are suited for this product.

ii) Neutral sulphite semichemical alder pulp is suitable for manufacturing insulation board, corrugation board and greaseproof paper.

iii) Red alder sulphate and soda pulps are suitable for printing paper, book paper, tissue paper and towelling paper. However, since alder pulp is resinous, bleaching is necessary. Douglasfir is the main species for sulphate pulping in the Pacific western forests. Alder sulphate pulp blended with the fir pulp produces paper that is light and takes a good finish; it is suitable for magazines, milk cartons etc. Fir pulp alone produces a bulky product with poor finish due to its large, coarse fibres.

Red alder wood is a source of cheap firewood because it is so abundant, it burns readily when well-dried, there is little ash and hardly any odour, sparking is minimal, and the wood is light and easy to saw into logs. The only fault of red alder as firewood is that it burns too quickly. It is also used to make charcoal.

Approximately 200 million board feet of red alder were logged in Oregon and Washington in 1959 (Worthington et al., 1962). Two-thirds of this was used for making pulp and the rest for furniture and miscellaneous uses.

In the light of the foregoing survey, one would predict a bright future for red alder in the Pacific northwest. Its economic value should increase and its status as a weed tree in British Columbia should vanish. The main characteristics in its favour appear to be:-

a) its nitrogen fixing capacity,

b) its rapid early growth,

c) its abundance and accessibility,

d) its suitability for lumber and pulpwood; blending with soft wood pulp seems promising especially since alder is closely associated with conifer over most of its range.

VII. Pests and diseases

The principal natural enemies of red alder are two fungi,

several leaf-eating insects, two aphid species and bark and wood-boring beetles.

a) _Fungi_

The most destructive is white heart rot, _Fomes igniarius_ (Fr.) Kickx., (Conners, 1967).

Didymosphaeria oregonesis Goodding causes stem cankers (Conners, 1967).

b) _Sucking insects_

There are two species of aphids, _Pterocallis alni_ (DeGeer) and _Euceraphis gillettei_ Davidson. _P. alni_ is well known (Browne, 1968).

c) _Leaf-eating insects_

There are two species of Chrysomelidae, _Altica ambiens_ Le Conte (Worthington, 1957; Keen, 1952) and _Pyrrhalta puncti-pennis_ (Mannerheim). The latter is not mentioned in any of the reviews of red alder.

Two species of tent caterpillars, _Malacosoma pluvialis_ Dyar and _Malacosoma disstria_ HBN. (Keen, 1952) occur on red alder.

Lastly two species of sawflies _Eriocampa ovata_ L. (Ross, 1951) and _Hemichroa crocea_ Fourcroy (Worthington, 1957) occur on red alder.

d) <u>Bark beetles and wood-boring beetles</u>

<u>Alniphagus</u> <u>aspericollis</u> (Le Conte) the alder bark beetle

is common (Fowells, 1965). There are several minor wood-

boring beetles that attack alder.

Red Alder on Burnaby Mountain

I. Site Characteristics

Burnaby Mountain has an elevation of 1200 ft. above sea level. The slopes on the north and western side are steep while the rest are more gentle and longer.

The parent material in the lower Fraser Valley is of glacial and post-glacial flood-plain origin (Kelley and Spilsbury, 1939). The soil on Burnaby Mountain falls into the Alderwood series on the basis of its colour, profile, drainage, and parent material. The Alderwood series is marked by several feet of hard boulder clay containing stones and gravel overlying deep layers of stratified sands and gravel. Two to four feet of surface alluvium complete the profile.

Observations on excavation sites on Burnaby Mountain and on cleared areas reveal that the soil is very sandy and, except where vegetation cover is dense and mulch has accumulated, the soil is generally very loose and unstructured in texture; it appears porous and conducive to leaching.

The mean monthly precipitation for Burnaby Mountain for the last five years is shown in Fig. II. The annual precipitation is usually above 80". The temperature regime in the Lower Fraser Valley is shown in Fig. III. Temperatures are fairly uniform in the Lower Fraser Valley (Kelley and Spilsbury,

Fig. II MEAN MONTHLY PRECIPITATION OVER A PERIOD OF 5 YEARS ON BURNABY MOUNTAIN

N.B.   BARS] INDICATE THE RANGE OF VARIATION
            OF PRECIPITATION OVER THE PERIOD
            OF 5 YEARS

Fig. III.   TEMPERATURE REGIME IN THE LOWER FRASER VALLEY

Temperatures are based on a 30 year average

(Kelley and Spilsbury, 1939)

1939).

The original forest of Burnaby Mountain was logged repeat-
edly commencing early in the century. Little of the original

forest remains.

Two types of vegetation zone can now be distinguished on

Burnaby Mountain, viz:-

a) a typical second-growth upland forest dominated by red

alder, western hemlock and western red cedar.

b) the areas that were cleared 5 years ago for construc-

tion of buildings and roads. Where unmanaged, these areas have

been invaded by dense stands of red alder saplings and several

shrubs.

A survey of the floristic composition of the two vegeta-

tion zones revealed the following:-

a) the older second-growth forest consists almost entirely

of the following:-

Red alder	- very abundant
Western hemlock	- abundant
Western red cedar	- abundant
Douglas-fir	- scattered
Broad-leaf maple	- less abundant
Vine maple	- less abundant

b) on the cleared areas the regeneration is almost entirely

made up of <u>Alnus</u> <u>rubra</u> Bong saplings. But there are a few species associated with it, mainly shrubs, viz:-

        Salmon-berry   - common

        Thimble-berry   - common

        Pacific willow (a tree) - common

        Bracken (a fern)   - common

The alder saplings constitute very dense stands. The associated species listed above are found only where the alder seedlings are about 1-2 years old and only a couple of feet tall. Where the saplings are older, the growth is very rapid and the red alder canopy cuts out overhead light to other seedlings as well as exhausting the food and water resources in the soil. Thus, an almost pure stand of very densely-packed older saplings results. There is almost nothing growing under the closed canopy.

The growth rate, in terms of the volume increments will be analyzed in detail in a later section. Defoliants have been applied to some of the alder stands in the past few years to check growth. No significant control of the regeneration resulted probably because the spraying was not sustained.

Project on Defoliation

Scope and Objectives

Though alder saplings seem to thrive on Burnaby Mountain,
by the end of summer, most trees are severely defoliated.

In the light of the earlier review of the economic status
of _Alnus rubra_ in the Pacific northwest, it seems useful to
study the impact on the growth of the species by the major
insects feeding on it. The general principles of what consti-
tutes economic damage are still not well defined (Strickland
et al., 1970; Stern et al., 1959). One reason is the difficul-
ty of objectively assessing the interaction between plant
growth and pest damage. Another reason is the presence of
many factors which have effect on growth; they are interrel-
ated in complex ways and studying one in isolation is unlikely
to yield meaningful results, for example:-

a) Buds and new foliage produce hormones which regulate
metabolic processes such as production of organic compounds
through photosynthesis, and the utilization of these compounds
for growth (Kulman, 1971). Therefore, if defoliation resulted
in fewer buds and less new foliage, lack of the necessary hor-
mones might stop utilization of stored food in the plant. This
could interfere with growth increment quite independently of

the reduction of photosynthetic surface, in which case, the direct effect of defoliation is on utilization of organic substances (Kozlowski and Keller, 1966).

b) The translocation of materials in the plant is very complex. At different times the lower and upper part of the stems may be acting as either a source or a sink for organic substances. Hence, the location of defoliation on the plant, and the time in the growing season when it occurs could influence growth in a complex fashion (Clausen and Kozlowski, 1967; Larson and Gordon, 1969).

c) Flower and fruit production may reduce foliage production and may thus confound the influence of defoliation on the area of photosynthetic surface (Kulman, 1971).

The impact of a complex of insects on plant growth and yield introduces even more factors to the system because the insects have differing feeding habits and differing life histories.

The scope of the present project was limited to defoliators only because the extent of the damage they cause can be estimated relatively quickly. The effect of the damage on the growth increment can be measured only approximately. One could hypothesize that although many factors influence growth, some weigh more heavily than others. Because the very heavy defol-

iation caused by the Chrysomelids and the sawfly by the end of the summer is the most conspicuous and drastic form of damage, it was considered plausible to study the effect of this component first.

Alder saplings constitute a suitable experimental subject because they grow rapidly and because some of the factors that complicate analysis of defoliation are absent in alder saplings. For example, there is no flower or fruit production by the saplings studied.

In practice, pest density rather than symptoms of pest presence, such as defoliation, is used for correlation with crop loss - and conversely, crop yield. Studying the effects of defoliation on the plant can be visualized as part of the overall study of productivity; and hence, it is theoretically important.

METHODS AND MATERIALS

I. The sampling site

A small stand of Alnus rubra covering about two acres on

the top of Burnaby Mountain was selected as a sampling site.

Because site characteristics greatly influence growth, a site

of relatively uniform elevation, aspect, and soil profile was

chosen. The stand consisted almost entirely of A. rubra sap-

lings between 3 and 5 years of age, and from 5 to 9 feet in

height, which had grown from seed following clearing of the

secondary forest about six years ago. All saplings were in

the phase of rapid growth. Sampling began in the summer of

1970 and continued the following year. In both years saplings

from the same age classes were sampled.

II. Visual estimation of defoliation

Toward the end of summer, 1970, the alder trees on Burn-

aby Mountain were heavily defoliated. But there was much

variation in the degree of defoliation of individual trees

even within the small experimental site; damage ranged from

virtually nil to nearly 100 percent defoliation.

Eighty-eight saplings representative of the various levels

of defoliation were selected and tagged with durable markers.

The first step was to estimate the total number of leaves

per tree by counting the leaves on representative branches and

multiplying by the number of branches, or branch equivalents,

on the tree. (For each sapling the total number of leaves

was expressed in terms of (x) branches, each branch bearing

approximately the same number of leaves; thus two or three

short upper branches were ranked as one (x) standard branch).

Twenty percent of the (x) branches, selected from all levels

and sides of the tree, were examined for leaf damage. Visual

estimates of damage to the leaf surface by insects were made.

The following data were recorded:-

a) Total number of leaves per sampled (x) branch

b) The number of (x) branches per tree

c) The number of undamaged leaves (in most samples this

was nil)

d) The number of leaves that had heavy, medium, or light

damage respectively, according to the proportion of

leaf surface damaged.

III. Check of visual estimation of defoliation

The three classes of damage, heavy, medium, and light

were subjective estimates. This kind of estimation is subject

to error but it is commonly used where more accurate measure-

ments would entail excessive labour and time. In this case,

precise measurements of surface areas and the areas of many

small holes in each sampled leaf seemed impractical. Thus the
less accurate visual estimate was used.

But some measure of the accuracy of this estimate seemed
desirable. Thus a sample of 4-5 leaves per tree were selected,
categorized into one of the three damage classes, and placed
in a plant press. The total areas of these leaves, and the
areas damaged were later measured by placing the pressed leaf
on 1 mm^2 graph paper and tracing around the margins of the leaf
and the damaged areas with a sharp, hard pencil. The respective
areas were then estimated by counting 1 mm squares contained
within the margins.

By these means a fairly accurate estimation of percentage
of leaf surface damage by insects was obtained. As these
leaves were previously categorized by visual estimate into
heavy, medium, and light defoliation classes, these classes
could now be checked against percentage defoliation. Thus
the consistency of the visual estimates could be checked and
could be given some meaning in terms of percentage defoliation.

The method of measuring leaf areas by counting squares is
slow and laborious, especially when leaves are heavily damaged
and there are many small holes. Some heavily damaged leaves
have lost a large proportion of their margins and it was nec-
essary to reconstruct the original leaf shape from rather

ragged remnants. This required a certain amount of guesswork.

Despite these deficiencies, this method was the most acceptable of those tried. Three other methods were considered and rejected.

i. Planimeter measurements - The planimeter was not sufficiently accurate to consistently measure the areas of the complex shapes of alder leaves and their damaged areas.

ii. Weight related estimates - Theoretically if the weight of an undamaged leaf is known, the weight loss of a damaged leaf could be correlated with surface area lost. There are a number of difficulties to application of the method: (a) Leaves of similar area vary in thickness, and therefore in weight. (b) Leaves collected were already damaged, thus the undamaged weight of the leaf was unattainable. (c) Not all damaged tissue is removed from the leaf, thus nonfunctional tissue is included in the weight of damaged leaves. (d) Leaves vary in thickness from base to tip, thus equal areas of tissue removed from base or tip correspond to unequal changes in weight. (e) The weights of leaves vary with moisture content and it is difficult to bring leaves to a uniform moisture content.

iii. Optical methods - A beam of light is passed through the leaf and the intensity of transmitted light is correlated

to degree of leaf area damaged. Differences of optical density of leaf tissue within and between leaves introduce experimental errors. Apparatus of sufficient sensitivity and accuracy was not available.

Thus the method of counting squares proved to be the simplest, most direct, and most accurate of suggested methods. But it is slow.

IV. Revised defoliation estimates

In 1971 the sampling program for estimating percent defoliation was modified to enhance the reproducibility of the estimates. Sample branches were selected from arbitrarily preselected sites on the stem one foot, two feet and three feet below the growing tip (when no branch occurred at precisely the measured distance, the nearest branch to the measured distance was selected). The total number of leaves and the number of leaves damaged per sample branch were recorded. Ten percent of the damaged leaves on each sample branch were selected, enclosed in a plastic bag, and the leaf area and area of damage were later measured by counting squares. These measurements were made while the leaves were still turgid to minimize variations of areas due to shrinkage of dried or wilted leaves. In addition the total number of leaves per sapling was counted in 1971. Only rarely, if ever, do insects

remove a complete leaf from an alder tree. Even when vir-
tually the entire leaf surface is destroyed, the petiole and
in main veins remain to be counted. In summer, however, with
the onset of hot, dry weather, some leaves fall. At the same
time growing tips are producing new leaves. Thus the total
number of leaves per tree is continually changing.

In spite of these confounding elements, the total number
of leaves on the tree at the time of each count was considered
to constitute the number born by the tree for the previous time
interval.

V. Measurements of seasonal growth

Tree growth was measured in terms of growth volume of
the main stem.

The main stem of the tree was considered to be made up of
a series of hollow cones fitted one over the other. Each cone
constitutes one year's growth. The first year's growth was
considered to be a solid cone. The volume of each cone was
calculated from the basal diameter of the tree at the end of
each growing season and the height attained by the tree in the
same season.

The stem of red alder saplings, especially those growing
in dense stands, is straight and erect, and it is close to
circular in basal section. Stems over three years old, however,

produce a terminal zone which is triangular in section. This part of the stem is very thin and constitutes an insignificant part of the total stem volume; for convenience this triangular form was ignored and the entire stem was considered conical in shape.

The numbers of and basal diameters of cones are readily obtained from the annual rings of the basal section. A disc of wood was sawn from the base of each stem and the face smoothed with a sharp chisel. Annual rings showed up as brown rings 5-10 minutes after cutting. These are caused by a sharp line of demarcation between large, thin-walled springwood cells and small, thick-walled summerwood cells of the same year. Occasionally false rings appeared. False rings are readily distinguished from true annual rings by microscopic examination of a microtome section stained with safranin.

Figs. IV-VII illustrate the gross morphology of the growth rings.

The heights of annual cones were obtained by splitting the stem longitudinally and noting the point where the number of annual rings decreases by one. This indicates the point where one year's longitudinal growth terminates.

From the height and basal diameter of cones, the total volume of the tree at the end of each year was calculated.

The annual volume measurement was obtained by subtracting

each year's total volume from the total volume attained the

previous year.

VI. Sampling for the vertical distribution of the main defolia-

tors

In July, 1971, the density of the principal defoliators,

P. punctipennis larvae and E. ovata larvae was high. Obser-

vations on P. punctipennis showed a scarcity of early instars

on the top half of the sapling. Also epidermal damage to the

leaves, attributed to early instars of P. punctipennis and A.

ambiens was more concentrated in the lower half of the sapling.

This suggested different feeding sites for different instars of

P. punctipennis larvae. To determine the vertical distribution

of Pyrrhalta larvae, 30 saplings averaging 3-4 feet were sel-

ected. Some were shaded and some fully exposed to light; they

also varied in the crown shape and vigour. Since E. ovata

larvae were important defoliators too and were abundant, they

were included in the sampling programme.

Each sapling was divided into foot intervals along the

vertical axis. For each interval, the following data was ob-

tained:-

    a) the total leaf number

    b) the number of damaged leaves

c) a visual rating of the extent of epidermal damage
    and perforation on the leaves; this was indicated
    by the symbols, x, xx, xxx, etc., a single x in-
    dicating the lowest rating

d) the total number of P. punctipennis and E. ovata

e) the number of early (mainly I) and late (II and III)
    instars of P. punctipennis

The subdivision of the saplings into intervals generally
resulted in individual branches falling into single intervals
because A. rubra branches are relatively horizontal in inclin-
ation. A. ambiens larvae were too scarce to justify inclusion
in the sampling programme. E. ovata larvae were mainly in
the early instars and they were not categorized into early
and late stages. Sampling was done over a wide range of day-
light hours.

Fig. IV.   Cross section of A. rubra stem under low power
                magnification to show the overall appearance
                of growth rings. The parenchyma rays are con-
                spicuous.

A

B

Fig. V.   Cross section of A. rubra stem stained with
            safranin. It shows the typical growth ring.
            The sharp contrast between the large xylem
            vessles of the springwood and the smaller
            elements of the summerwood is also illustrated.

                 Magnification: x 25

Fig. VI.   Cross section of <u>Alnus</u> <u>rubra</u> Bong stem stained
with safranin. Figure shows a rare type of
false ring which causes the true ring to appear
double under low power magnification.

Magnification: x 25

Fig. VII.   Cross section of <u>A</u>. <u>rubra</u> stem stained with
safranin to show the hazy discontinuous aspect
of two false rings under low power magnifica-
tion. This type of false ring is common on
<u>Alnus</u> stem sections. To the naked eye the
false rings appear just a shade fainter than
the rest of the rings and could be confused
for true rings.

Magnification: x 25

RESULTS

Classification of late summer (August and September, 1970) damage into visually estimated damage classes is shown in Table 2. Table 2 shows the mean number of leaves sampled per sapling, the mean number of leaves falling into each damage class and the number of whole trees falling into each damage class.

Estimates of defoliation done by careful measurements of leaf areas and areas of leaf damage are shown in Tables 3 and 4. The tables show the calculated percentages of leaf surface damaged.

The visual and measured defoliation indices for 1970 were compared (Fig. VIII). It is apparent that there is much discrepancy between the two. Hence visual impression of the severity of defoliation are deceptive.

Both in the fall of 1970 and in the summer of 1971, measurements of leaf damage on A. rubra saplings entailed:-

a)   an estimate of the percentage of leaf surface area destroyed by defoliators at each sampling date (Fig. IX).

b)   an estimate of the total number of leaves per sapling at each sapling date. Using a mean leaf size the total photosynthetic surface per sapling was calculated (Table 5). Figs. XA and XB show the pattern of change of the two variables.

Fig. VIII Relationship between visual and measured damage to leaves

c) an estimate of the proportion of leaves damaged per sampling date (Fig. XI and Table 6).

Figures XA and XB reveal that maximal leaf surface area per sapling was achieved about the end of June, 1971. Before the end of June the production of new leaves at the growing tips was high. In July and August a moderately high and persistent leaf-fall was noted. Though no precise measurement of leaf production or loss were made, before mid-summer new leaf production apparently exceeds leaf-fall while after mid-summer leaf-fall apparently exceeds new leaf production.

Figure XI shows that very few leaves were damaged prior to June, 1971, and of those leaves damaged, an almost imperceptible portion of the leaf surface was destroyed by defoliators (Fig. IX).

Although the number of leaves attacked by defoliators increased rather dramatically in late June and July, the extent of the damage per leaf remained low well into August. Figure XII shows the seasonal change in the proportion of leaves damaged superimposed on the percentage of leaf area damaged. Between June and July about 20% of the leaves were damaged but the area of leaf surface destroyed remained under 3%.

The percentage of leaf surface destroyed shows a sharp

FIG. IX   SEASONAL CHANGE IN MEAN PERCENT LEAF AREA DAMAGED BY INSECTS

FIG X.   (A). CHANGE IN MEAN SURFACE AREA PER STEM
          (B). CHANGE IN MEAN NUMBER OF LEAVES ON STEM

FIG XI. SEASONAL DISTRIBUTION OF PERCENTAGE OF RED ALDER LEAVES DAMAGED BY DEFOLIATORS

FIG. XII   RELATIONSHIP BETWEEN   THE   NUMBER   OF

DAMAGED LEAVES AND PERCENT AREA DAMAGED

upward trend in August and reaches a maximum in late August.

Leaf damage was not evenly distributed throughout the total foliage of the tree. Many leaves received no damage, as indicated by the low proportion of leaves showing damage until late August 1971. Of the leaves damaged, there was a predominance of leaves with very slight damage and a very few leaves with heavy damage (Figs. XIII-XVIII).

The distribution of the agents causing damage showed that the number of first instar larvae of P. punctipennis decreased with increasing height on the stem. Thus damage by this defoliator tended to be confined to the lower and more shaded branches. The remaining instars of P. punctipennis and all instars of E. ovata were widely scattered throughout the crown, (Figs. XIX-XXI).

Volume increment data obtained in the fall of 1970 is shown in Table 7. Percentage increment rather than gross volume increment was considered more suitable for comparison of yields to eliminate variance of gross volume growth introduced by differences in initial tree size (Table 8). Table 8 shows mean percentage increase in wood volume of very high magnitudes; a five-fold increase for 3 year old saplings and a three-fold increase for 4 year old saplings.

The relationship between total defoliation at the end of

the season and volume increment of the stem over the season
showed no correlation (Fig. XXII). Also there was no sig-
nificant correlation between the residual leaf surface and
volume increment (Figs. XXIII and XXIV).

FIG. XIII
FREQUENCY   DISTRIBUTION   OF   DAMAGE   TO   LEAVES

OF   RED   ALDER.   21 vi 71.

FIG, XIV   28vi 71. FREQUENCY DISTRIBUTION OF DAMAGE TO LEAVES OF RED ALDER.

No of leaves

Area of leaf damaged (sq mm)

FIG. XV   8 vii 71. FREQUENCY   DISTRIBUTION   OF

DAMAGE TO LEAVES OF RED   ALDER.

FIG. XVI   15 VII 71. FREQUENCY DISTRIBUTION OF

DAMAGE TO LEAVES OF RED ALDER.

FIG. XVII   22 vii 71. FREQUENCY   DISTRIBUTION   OF

DAMAGE   TO   LEAVES OF RED ALDER.

No of leaves

16

14

12

10

8

6

4

2

0

0-50
51-100
101-150
151-200
201-250
251-300
>300

Area   of   leaf   damaged (sq mm)

FIG. XVIII   6 viii 71, FREQUENCY   DISTRIBUTION   OF

DAMAGE   TO LEAVES OF RED ALDER.

No of leaves

16

14

12

10

8

6

4

2

0

O—50   51—IOO   IOI—I50   I5I—2OO   2OI—25O   25I—3OO   >3OO

Area of leaf damaged (sq mm)

FIG. XIX FREQUENCY DISTRIBUTION OF

P. PUNCTIPENNIS FIRST INSTARS ON STEMS

FIG. XX FREQUENCY DISTRIBUTION OF LATE INSTARS OF P. PUNCTIPENNIS ON STEM

FIG. XXI FREQUENCY DISTRIBUTION OF E. OVATA LARVAE ON STEM

FIG. XXII RELATIONSHIP BETWEEN MEAN PERCENT DEFOLIATION AND WOOD VOLUME INCREMENT

$r = -0.1$

PERCENT OF LEAF DAMAGED

50 40 30 20 10

VOLUME INCREMENT (CU.CM.)

100 200 300 400 500 600 700

FIG. XXIII RELATIONSHIP BETWEEN WOOD VOLUME
INCREMENT AND RESIDUAL LEAF AREA
IN THREE–YEAR OLD STEMS

r = –0·5

Fig. XXIV RELATIONSHIP BETWEEN WOOD VOLUME

INCREMENT AND RESIDUAL LEAF AREA

IN FOUR-YEAR OLD STEMS

$r = 0.04$

AREA (SQ. CMS)

Notes on Insects Occurring on Red
Alder on Burnaby Mountain

I. <u>Pyrrhalta</u> <u>punctipennis</u> (Mannerheim)(Chrysomelidae)

The genus <u>Pyrrhalta</u> has been revised twice. This spe-
cies was previously assigned to the <u>Galerucella</u> and <u>Tricho-
lochmaea</u>. The current name, <u>P</u>. <u>punctipennis</u> is after Wilcox
(1965).

<u>P</u>. <u>punctipennis</u> is extremely abundant on <u>A</u>. <u>rubra</u> on
Burnaby Mountain. Surveys of the population at various sites
on the mountain showed that the distribution was markedly
clumped. There were high densities on open stands consisting
of young short alder saplings of the order of 2-4 feet. In
contrast, older stands which were dense had very low densities.
Densities of 10-20 per sapling adults were common on the short
saplings. Adults were numerous during the months of May and
June in 1971 and then the numbers began to decline. Adult
numbers increased again in mid-August.

<u>P</u>. <u>punctipennis</u> adults were observed feeding, on alder
foliage, in April. They appeared very soon after the red
alder had acquired new foliage. Eggs were obtained from adult
beetles reared on alder leaves in petri dishes. Fresh leaves
were supplied every second day. The female lays round, whitish-
yellow eggs, scattered over the leaf surface (Fig. XXV). Where

Fig. XXV   Eggs of P. punctipennis

          Magnification: x 5

the adults were reared on alder twigs bearing several tiers
of leaves the females showed preference for the lowest leaves
i.e. the base of the twig. Incubation lasts about one week.

The first instar larvae are greyish-black but the later
instars are yellowish with black stripes across the abdominal
segments (Fig. XXVI). P. punctipennis development passes
through a first, second and third instar and then a pre-pupa
and pupa stages. The development from egg to adult takes 35-
40 days, approximately. There are two generations in a year.

The early instars feed mainly on the leaf epidermis and
the patches thus made later turn yellowish brown. They are
concentrated on the lower branches and feed on the ventral
leaf surfaces. The older larvae chew away round holes on
the leaf surface (Fig. XXVI). They are scattered more widely
on the crown. Adults similarly eat away round holes on the
leaf (Fig. XXVII). The adults, unlike the larvae, feed mainly
on the dorsal side of the leaf. Many adults were observed
feeding in groups of 2-10 on single leaves. The net effect
of the eating away of many small holes is to skeletonize the
leaf. Adult P. punctipennis appear to prefer feeding on
short young saplings and also on the terminal leaves of taller
saplings.

Fig. XXVI   <u>Top</u>: Characterisitic circular holes
                         eaten off by large larvae of
                         P. <u>punctipennis</u>

            <u>Bottom</u>: A third instar larva of P.
                         <u>punctipennis</u>

Fig. XXVII   Comparison of leaf damage caused by
adult Chrysomelids.

Leaves marked (A) show isolated holes
eaten off by A. ambiens.

Leaves marked (B) show the concentrated
feeding of P. punctipennis.

this feature and were generally larger than the males.

B. pun... larvae were obser... ... on leaves

of black ... Populus tric... and

balsam p... balsami...

1. Altica ... the ...

Haltica w... na... ... ambiens is

commonly known as the alder flea ... native to the

Pacific coast ... It occurs also on other coastal hard-

wood ... being common or

... ... very com-

... Washington ...

... ively ...

... A. ambi...

... summer. ...position occurs ar...

April but it is spread over sever...

overlapping generations.

Early instars of A. ambiens feed on the epidermis on

the lower side of the leaf; the patches fed on then turn brown

Males were distinguished from females by the pyramidal

cleft on the last sternite (Fig. XXVIII). The females lacked

this feature and were generally larger than the males.

P. punctipennis larvae were observed feeding on leaves

of black cottonwood (Populus trichocarpa Torr. et Gray) and

balsam poplar (Populus balsamifera L.)

II. Altica ambiens Le Conte (Chrysomelidae)

Haltica was the older name for the genus. A. ambiens is

commonly known as the alder flea beetle. It is native to the

Pacific coastal states. It occurs also on other coastal hard-

wood such as poplar and willow, in addition to being common on

red alder (Keen, 1952). A. ambiens was reported as very com-

mon on red alder (Worthington, 1957; Keen, 1952) but on Burn-

aby Mountain it is relatively scarce.

The low density of A. ambiens persisted through spring

and summer. Oviposition occurs after about one week of feeding

in April but it is spread over several weeks. This results

in overlapping generations.

Early instars of A. ambiens feed on the epidermis on

the lower side of the leaf; the patches fed on then turn brown

(Fig. XXIX). Older larvae eat away small holes in the leaf

leaving the small veins intact (Fig. XXIX). This skeletonizing

habit appears to be characteristic. Adults also eat away holes

Fig. XXVIII   A. Dorsal view of adult P. punctipennis.

                B. Ventral view of adult P. punctipennis
                    showing the cleft on the last sternite
                    of the male (left).

                    Magnification: x 8

A

B

Fig. XXIX   Top: Third instar larva of <u>Altica</u> <u>ambiens</u> Le-
conte. The greyish black colour and black
tubercles readily distinguish the larvae
from those of the other Chrysomelid occupy-
ing the same niche i.e. <u>P</u>. <u>punctipennis</u>.

          Middle: Brown patches on leaf surface indicate
epidermal damage by young <u>A</u>. <u>ambiens</u>
larva. Young <u>P</u>. <u>punctipennis</u> larva
cause similar damage.

          Bottom: Holes made by older <u>A</u>. <u>ambiens</u> larva tend
to be more rectangular than circular.
Often veinlets are left intact giving rise
to a reticulate pattern to the damaged
surface of the leaf.

in the leaf, but they do not generally leave the small veins

intact.

A Tachinid parasite was collected from an adult A. ambiens

in May, 1971 but continued observation of laboratory cultures

of adult beetles did not yield more parasite specimens. There

is no previous record of parasitism on A. ambiens. The Tach-

inid imago is shown in Fig. XXX.

III. Eriocampa ovata L.

The red-backed sawfly, E. ovata, is widespread on Alnus

spp. throughout Canada (Ross, 1951; Raizenne, 1957; Bouchard,

1960). It is bivoltine and reproduces parthenogenetically

(Bouchard, 1960). On Burnaby Mountain it was found to be

bivoltine and to reproduce pathenogenetically; it passes

through 6 or 7 instars which defoliate A. rubra foliage heavily

leaving only the midrib and secondary veins (Borden and Dean,

1971).

In 1971 early instars of E. ovata were observed in large

numbers in late June but the 1971 population was much smaller

than the 1970 one for the remainder of the summer and in the

fall. Sawfly larvae were more abundant on the lower and middle-

level branches of the alder saplings. Fig. XXXI shows a mid-

instar larva of E. ovata and the nature of the damage it

causes on alder leaves.

Fig. XXX.   A. Adult <u>A</u>. <u>ambiens</u> specimen with the
                  tachinid parasite pupa still attached
                  to the lateral posterior side of the
                  abdomen.

              B. Dorsal view of the tachinid imago.

                  Magnification: x 8

A

B

Fig. XXXI.   A.   Mid-instar larva of <u>Eriocampa</u> <u>ovata</u> L.
     (topmost) showing the characteristic white exuviae
              that larval instars except the last one
              exhibit.

            B.   Early damage by <u>E</u>. <u>ovata</u> larva. Exten-
              sive feeding at one point on the surface
              before moving on produces the large ir-
              regular holes.

            C.   Extreme damage by <u>E</u>. <u>ovata</u> larva. By the
              end of summer the damaged leaves are large-
              ly reduced to this level of defoliation,
              <u>E</u>. <u>ovata</u> being the main defoliator late in
              the season.

IV. Hemicroa crocea Fourcroy (Tenthredinidae)

The striped alder sawfly appears very rare on Burnaby Mountain red alder. Late instar larvae were collected from young saplings at a site near the University Buildings on 22nd July, 1971. No other specimens were found on A. rubra locally. The larvae died after two days during which they fed voraciously on excised alder leaves. They changed from the original yellow colour broken by dark stripes into a pale dark colour; the cuticle also appeared shrivelled, as if the body contents were disintegrating. This, coupled with the simultaneous death suggested the larvae may have had a disease. Fig. XXXII shows a late instar larva of H. crocea.

V. Malacosoma pluvialis Dyar

M. pluvialis, the western tent caterpillar is common in the Pacific northwest especially on alder. A colony of larvae was observed in early June, 1971. The larvae were reared on alder leaves through the pupa stage but no adults emerged, since parasitization by a Braconid was 100%.

Fig. XXXII.   Mature larva of <u>Hemichroa</u> <u>crocea</u> Fourcroy. The lateral stripes are a characteristic feature.

Magnification: x 8

DISCUSSION

The object of the research was to define the effect of defoliation by insects on _A. rubra._ Seasonal growth increment as indicated by wood volume was considered a suitable parameter for correlation with defoliation index. This is because the stem is the economically important product of _A. rubra._ Also wood increment is the best measure of cellulose production by woody plants. Therefore, the study would be of theoretical interest from the standpoint of productivity in plant ecosystems.

One of the important factors in crop production is the evaluation of the economic threshold of pest damage. Pest management resources can be meaningfully applied if, and only if, the economic threshold level is determined. The project on red alder could be visualized as a simulation of a crop production situation. Thus, analysis of the impact of defoliators on the growth of alder saplings is here considered the first step in the determination of economic threshold of insect damage.

Red alder on Burnaby Mountain is conspicuously defoliated by two Chrysomelids and a sawfly. The intensity of damage varies from year to year, thus in 1970 it was much higher than

in 1971, but is is normally sufficiently high to warrant
speculation that it may harm the host plant. It was alarm-
ingly high by late summer in 1970. A similar level of ap-
parent damage to a commercial forest plantation or agricultur-
al crop would almost certainly call for insect control measures,
at least in keeping with the prevailing philosophy of pest
control.

Visual estimates of defoliation are unreliable as shown
in Fig. VIII. For example, saplings with "heavy" defoliation
had as little as 30% loss of leaf surface and a maximum loss
of 85%. Those with "light" defoliation had as much as 27%
loss of leaf surface. Therefore, visual estimations of leaf
damage are a poor criterion of leaf surface lost to insects
in this example.

The lack of normalcy in the distribution of leaf damage
probably contributes to the wide margin of error in the visual
estimates. Damaged leaves are not randomly distributed through-
out the tree. Also the amount of damage per leaf is not ran-
domly distributed throughout the damaged leaves. The distri-
bution of damaged leaves is probably closely linked with the
chronology and mobility of the defoliating agents and in ad-
dition to these factors, the feeding behaviour of the defol-
iators might determine the distribution of the amount of dam-

age per leaf.

First instar and young second instar larvae of P. puncti-
pennis were prevalent on the lower level branches. Older in-
stars of this Chrysomelid have more vertical mobility and
thus scatter leaf damage over the whole stem. However, E.
ovata larvae, which like P. punctipennis larvae, eat holes in
the leaf, may concentrate rather than scatter leaf damage.
E. ovata larvae have relatively less vertical mobility. They
feed voraciously at a given site before moving on to the next
leaf. On tall saplings, above 4 feet in height, E. ovata ap-
pear to concentrate on the lower and middle level shaded
branches whereas adult P. punctipennis appear to prefer feed-
ing on the exposed leaves.

The seasonal change in the population density of the de-
foliators is another factor that determines the degree and
distribution of damage both on individual stems and in a
given area. Thus, for example, A. ambiens were limited to very
few sites on Burnaby Mountain and its contribution to defolia-
tion was not studied in as much detail as was that of P. puncti-
pennis and E. ovata. P. punctipennis adults were abundant by
May in 1971. In June there was a large population of adults
and larvae. Adults then began to decrease in numbers until
mid-August when second generation adults appeared in large

numbers. E. ovata larvae showed a steady build up from the beginning of July in 1971 and by early August were very abundant. Thus, the contribution of P. punctipennis larvae and adults begins early and builds up to a peak in August. The sawfly damage supplements the Chrysomelid damage later in the summer. The smaller numbers in 1971 might explain the markedly high overal damage on red alder in late 1971.

Between mid-June and late fall foliage area per tree appeared to be on the decline as shown in Fig. XA. The sharp drop in leaf surface between mid-June and mid-July in 1971 was probably due to the dry, hot weather and normally the decline in foliage area would be expected to be more gradual. However, the early start of the decline in leaf surface area was an unexpected finding. Though measurement of the chronology of stem increments were not made, it is known that the formation of springwood cells is complete by mid-summer. Springwood constitutes the bulk of the wood volume increment. It is probable that there is a relationship between these two events. After mid-summer, the stem growth consists of summerwood. Because total leaf surface is on the decline during this period, it may be that the spring flush of leaves produces a photosynthetic surface surplus to the summer needs of the tree.

Virtually no insect damage occurred until after mid-summer. From mid-June to mid-August the number of damaged leaves increased, up to 20% of the leaves showing visible damage. But the average damaged areas remained small (less than 10% of the total leaf surface) until mid-August. Thus, there was little loss of foliage to insects until mid-August, by which time most of the summerwood production is complete. Significant leaf damage began to occur in late August and early September.

Because the decline in leaf surface area resulting from factors other than insect defoliation appears to overshadow the relatively small loss caused by defoliators, one would not expect to find any correlation between late summer defoliation and stem increment. No such correlation could be established. Nor would one expect a correlation between insect defoliation and stem growth at any other period in the growing season, because little defoliation occurred before late summer.

If the amount of foliage lost over the summer did not affect stem growth, one might expect that stem growth would be related to the residual foliage on the tree. But no significant correlation between these variables was found either.

It is thus concluded that there was not direct relationship between the amount of foliage left on the tree at the

end of the growing season and the amount of stem growth.

Williams (1971) working on A. rubra seedlings found that

total plant photosynthesis reaches a maximum in late summer;

translocation patterns indicated that most of the carbohydrate

produced then tends to be stored in the roots where it provides

the source of material for the spring flush of growth. Hence,

a complex of physiological processes exists and one would need

to study all the key components in the system to get a complete

picture.

The amount of photosynthesis carried on by the tree would

appear to be a key component to the tree's welfare. It seems

probable that this would be related to the gross area of photo-

synthetic surface. But a number of additional questions could

be asked. To what degree does leaf damage interfere with photo-

synthesis and translocation of the remaining portion of the leaf?

In what manner does the gross photosynthetic area influence

a tree's growth? How much of a tree's foliage is essential

for normal growth, and how does this change over the season?

Leaf area represents not only photosynthetic area, but also

respiratory area and translocation area. What sort of changing

balance is maintained between these processes as the physical

environment changes with the advancing season? A search of

literature reveals little information on this subject. It seems rather important in relation to the potential of phytophagous animals to injure the tree or to limit its growth. It would certainly have an effect on determination of the economic threshold of damage. An investigation of these questions would be an appropriate subject for further study.

CONCLUSIONS

1. The red alder on Burnaby Mountain is attacked by three main defoliating insects:

a) _Pyrrhalta punctipennis_ (Mannerheim)

b) _Eriocampa ovata_ L.

c) _Altica ambiens_ Le Conte

2. These insects cause virtually no damage to leaves of _A. rubra_ before mid-summer. After mid-summer visible damage becomes apparent. Up to about 20% of the leaves are damaged but the areas of damage are small and less than 3% of the total surface is lost before August.

3. A progressive decline in photosynthetic surface area of _A. rubra_ saplings was found between mid-June and the fall. It is likely due to an excess of leaf fall, pronounced in dry hot weather, over leaf production.

4. Severe defoliation of _A. rubra_ by these insects does not occur until late fall. After which time, stem growth is virtually, if not totally, completed for the season.

5. No relationship was established between leaf surface lost to defoliators and the stem wood volume increment.

6. No relationship was established between leaf surface remaining in the tree at the end of the season and stem wood volume increment.

7.   Thus, defoliation of A. rubra by these insects, though apparently high during some years, does not appear to have any direct effect on stem wood volume increment in the current year.

LITERATURE CITED

1. Bond, G. 1956. Evidence for fixation of nitrogen by root nodules of alder (Alnus) under field conditions. New Phytologist 55(2): 147-153

2. Borden, J.H. and W.F. Dean. 1971. Observations on Eriocampa ovata L. (Hymenoptera:Tenthredinidae) infesting red alder in southwestern British Columbia. Jour. Ent. Soc. B.C. 68(1971): 26-28.

3. Bouchard, P. 1960. La tenthrede a thorax rouge de l'aulne, Eriocampa ovata L. (Hymenoptera:Tentheridinidae). Ann. Soc. Ent. Que. 6: 69-80.

4. Browne, F.G. 1968. Pests and Diseases of Forest Plantation Trees. Clarendon Press, Oxford.

5. Clausen, J.J. and T.T. Kozlowski. 1967. Food sources for growth of Pinus resinota shoots. Advan. Frontiers Plant Sci. 18:23-32.

6. Conners, I.L. 1967. An Annotated Index of Plant Diseases in Canada. Research Branch, Canada Department of Agriculture Publication 1251.

7. Crocker, R.L. and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. Jour. Ecol. 43: 427-448.

8. Fowells, H.A. 1965. Silvics of forest trees of the United States. Agric. Handb. 271. Washington, D.C.

9. Hetherington, J.C. 1964. Brush control in coastal British Columbia. Research notes. British Columbia Forest Service No. 38.

10. Johnson, F.D. 1968. Taxonomy and distribution of northwestern alders. In: Biology of Alder. Trappe, J.M. et al (eds). pp. 9-22. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon.

11. Keen, F.P. 1952. Insect enemies of western forests. U.S. Dept. Agr. Misc. Pub. 273.

12. Kozlowski, T.T. and T. Keller. 1966. Food relations of
        woody plants. Bot. Rev. 32: 293-382.

13. Kulman, H.M. 1971. Effects of insect defoliation on
        growth and mortality of trees. Annual Review of
        Entomology 16: **289-323.**

14. Kelley, C.C. and R.H. Spilsbury. 1939. Soil survey of
        the Lower Fraser Valley. B.C. Dept. Agr. Soil
        Survey Report No. 1.

15. Larson, P.R. and J.C. Gordon. 1969. Leaf development,
        photosynthesis, and C^{14} distribution in Populus
        deltoides seedlings. Am. J. Bot. 56: 1058-1066.

16. Raizenne, H. 1957. Forest sawflies of southern Ontario
        and their parasites. Can. Dept. Agrig. Publ.
        No. 1009.

17. Rodriguez-Barrueco, C. and G. Bond. 1968. Nodule endo-
        phytes in the genus Alnus. In: Biology of Alder.
        Trappe, J.M. et al (eds.). pp. 185-191. Pacific
        Northwest Forest and Range Experiment Station,
        Forest Service, U.S. Department of Agriculture,
        Portland, Oregon.

18. Ross, N.N. 1951. In: Hymenoptera of America North of
        Mexico. Musebeck, C.F.W. and K.V. Krombern (eds.).
        U.S. Dept. Agric. Mon. No. 2.

19. Stern, V.M., R.F. Smith, R. Van den Bosch and K.S. Hagen.
        1959. The integrated control concept. Hilgardia
        29: 81-101.

20. Strickland, A.N., E.J. Moore and L. Chiarappa. 1970.
        Crop loss assessment methods. Food and Agricul-
        ture Organizations of the United Nations. Rome,
        1970.

21. Tarrant, R.F., L.A. Isaac and R.F. Chandler. 1951. Ob-
        servations on litter fall and foliage nutrient
        content of some Pacific Northwest tree species.
        Jour. Forestry 49: 914-915.

22. Tarrant, R.F. 1961. Stand development and soil fertility
         in a Douglas-fir and red alder plantation. Forest
         Sci. 7: 238-246.

23. Tarrant, R.F. 1963. Accumulation of organic matter and
         soil nitrogen beneath a plantation of red alder
         and Douglas-fir. Soil Sci. Soc. Amer. Proc. 27:
         231-234.

24. Tarrant, R.F., C.T. Dyrness, D.G. Moore and J.F. Franklin.
         1968. Chemical soil properties under coastal
         Oregon stands of alder and conifers. In: Biology
         of Alder. Trappe, J.M. et al (eds.). pp. 157-172.
         Pacific Northwest Forest and Range Experiment
         Station, Forest Service, U.S. Dept. of Agriculture,
         Portland, Oregon.

25. Williams, A.M. 1971. Personal communication.

26. Wilcox, J.A. 1965. A synopsis of the North American
         Galerucinae. N.Y. Mus. and Sci. Service Bull.
         400.

27. Worthington, N.P. 1957. Silvical characteristics of
         red alder. U.S. Forest Services, Pacific North-
         west Forest and Range Experimental Station.

28. Worthington, N.P., R.M. Ruth and E.E. Matson. 1962.
         Red alder, its management and utilization. U.S.
         Dept. Agr. Misc. Pub. 881.

29. Yamaya, K. 1968. On the influence of alder (Alnus
         inokumae) on soil properties in northern Japan.
         In: Biology of Alder. Trappe, J.M. et al (eds.).
         pp. 197-207. Pacific Northwest Forest and Range
         Experiment Station, Forest Service, U.S. Dept. of
         Agriculture, Portland, Oregon.

TABLE 2.   Visual estimates of the degree of defoliation on

red alder leaves in the fall of 1970

Date of sampling	Mean total number of leaves per stem	Mean number of leaves damaged per stem	Mean number of leaves in the damage classes: Heavy (H)	Medium (M)	Light (L)	Mean number of damage classes for all stems per sampling date (H)	(M)	(L)
17 VIII 70	381 ± 103 (S.E)*	74 ± 20	55 ± 14	55 ± 14	4 ± 2	3	2	0
29 VIII 70	355 ± 44	71 ± 8	25 ± 14	23 ± 4	13 ± 5	8	2	1
30 VIII 70	662 ± 109	127 ± 17	85 ± 14	27 ± 5	15 ± 3	1	0	0
31 VIII 70	742 ± 142	113 ± 19	74 ± 18	26 ± 3	12 ± 3	5	2	1
1 IX 70	587 ± 99	104 ± 16	14 ± 2	71 ± 13	19 ± 4	0	2	8
2 IX 70	574 ± 56	101 ± 10	34 ± 7	54 ± 8	17 ± 2	1	5	4
8 IX 70	364 ± 102	53 ± 13	16 ± 4	30 ± 10	6 ± 1	3	5	1
9 IX 70	386 ± 29	73 ± 5	36 ± 4	21 ± 3	13 ± 2	2	6	1
10 IX 70	321 ± 39	56 ± 7	20 ± 5	23 ± 3	12 ± 2	5	3	7

N.B.   * ± in all instances refers to the standard error (S.E)

TABLE 3.   Data on mean leaf areas, mean damaged leaf areas

and the mean defoliation percentages for

<u>A. rubra</u> saplings in 1970

Date of sampling	Mean total leaf area (sq mm)	Mean area of leaf damaged (sq mm)	Mean percent of leaf area damaged
17 VIII 70	5478 ± 431 (S.E)*	2978 ± 531	54%
29 VIII 70	4088 ± 283	1199 ± 323	29%
30 VIII 70	6307 ± 310	2385 ± 284	37%
31 VIII 70	5360 ± 401	2581 ± 493	48%
1 IX 70	5020 ± 354	571 ± 100	11%
2 IX 70	4945 ± 191	1520 ± 238	30%
8 IX 70	4853 ± 251	1691 ± 225	34%
9 IX 70	6831 ± 363	2358 ± 271	34%
10 IX 70	5610 ± 254	1467 ± 217	26%

N.B.   * ± refers to the standard error (S.E)

TABLE 4.   Data on mean leaf areas, mean leaf areas damaged

and the mean defoliation percentages for

A. rubra saplings in 1971

Date of sampling	Mean total leaf area (sq mm)	Mean area of leaf damaged (sq mm)	Mean percent of leaf area damaged
21 VI 71	4810 ± 278 (S.E)*	77.3 ± 19.1	1.6%
28 VI 71	6067 ± 423	53.80 ± 14.4	0.87%
8 VII 71	6674 ± 395	57.0 ± 19.0	0.85%
15 VII 71	5672 ± 314	86.7 ± 16.0	1.53%
22 VII 71	4969 ± 305	111.7 ± 23.7	1.79%
6 VIII 71	5180 ± 163	123.4 ± 13.3	2.38%

N.B.   * ± refers to standard error (S.E)

TABLE 5.   The seasonal change in the mean number of leaves

per stem and the mean total photosynthetic

surface per stem

Date	Mean number of leaves per stem (running averages)	Mean leaf size area (sq cm)	Total photosyn-thetic surface (sq cm)
17 VIII 70	498	5478	27×10^3
29 VIII 70	368	4088	15×10^3
30 VIII 70	508	6307	32×10^3
31 VIII 70	702	5360	37×10^3
1 IX 70	664	5020	33×10^3
2 IX 70	580	4945	26×10^3
8 IX 70	469	4853	20×10^3
9 IX 70	375	6831	25×10^3
10 IX 70	353	5610	19×10^3
21 VI 71	1134	4810	54×10^3
28 VI 71	980	6067	59×10^3
8 VII 71	635	6674	42×10^3
15 VII 71	574	5672	32×10^3
22 VII 71	642	4969	31×10^3
6 VIII 71	598	5180	31×10^3

TABLE 6.   <u>Seasonal change in the mean percentage of the</u>
<u>total foliage per sapling that is</u>
<u>damaged by defoliators</u>

Date	Mean % leaves damaged	Standard Deviation
17 VIII 70	97.3	6.33
29 VIII 70	86.2	13.90
30 VIII 70	92.39	6.42
31 VIII 70	87.4	16.23
1 IX 70	88.2	8.77
2 IX 70	86.5	8.40
8 IX 70	92.6	5.60
9 IX 70	89.3	15.2
10 IX 70	83.5	14.3
21 VI 71	25.7	14.69
28 VI 71	30.20	14.91
8 VII 71	23.7	14.39
15 VII 71	37.2	18.80
22 VII 71	43.7	15.8
6 VIII 71	87.7	13.46

TABLE 7.   Seasonal wood volume increments in red alder
saplings aged 2 - 4 years

The terminal figures in each horizontal row represent yields
during the season ending in fall, 1970. Volumes are
expressed in cubic centimeters.

1st Year	2nd Year	3rd Year	4th Year
24.8	205.35		
8.80	50.36	54.24	
4.49	29.45	123.20	
5.13	54.41	181.28	
7.72	43.91	217.45	
10.05	149.17	812.84	
29.03	285.22		
15.5	53.3	148.1	
4.2	64.5	320.8	
22.4	186.8	405.8	
7.0	58.8	498.2	
18.3	122.1	361.9	
25.2	205.6		
10.6	87.2	301.1	
9.6	64.1		
8.80	74.9	237.2	
10.1	45.4	103.3	
0.5	19.5	97.2	250.8
0.25	31.2	159.2	322.3
0.20	28.9	150.6	698.7
0.9	23.9	91.8	195.9
0.6	19.6	158.7	674.1
0.3	41.9	229.9	631.0
0.4	13.9	79.6	345.7
16.8	22.2	512.0	
0.5	25.0	78.3	289.5
0.4	17.6	121.5	324.0
0.3	10.9	134.9	320.3
0.7	28.4	144.8	333.1
19.2	167.9	608.5	
0.4	12.4	99.8	397.2
19.6	90.9	319.8	
2.2	35.9	211.5	654.0
22.9	119.0	310.3	
1.0	13.0	85.8	338.6
9.9	390	198.0	
0.5	17.3	80.2	320.1
1.9	40.2	102.3	
0.5	50.56	223.62	375.1
1.9	33.4	116.7	
1.1	27.3	182.8	471.5
4.6	44.6	159.2	
1.0	14.4	103.2	
1.4	20.7	124.9	
0.3	18.1	54.7	36.5

TABLE 7. (Cont'd)

1st Year	2nd Year	3rd Year	4th Year
1.5	44.4	77.1	198.4
0.30	37.2	106.5	153.4
0.20	13.1	78.0	250.2
0.5	20.3	69.7	118.6
0.6	31.9	121.2	314.2
18.20	51.5	164.7	
0.6	12.0	51.2	105.1
0.2	14.4	52.9	94.6
0.10	9.6	60.4	219.0
0.40	23.8	103.1	168.1
0.2	5.4	43.1	74.9
0.3	3.4	18.5	77.4
0.1	3.2	18.5	51.3
0.1	7.9	26.5	60.0
0.2	14.7	20.3	233.4
0.1	10.1	40.1	86.4
2.9	13.4	71.4	
2.8	93.9	210.7	
1.4	58.3	165.7	
0.6	6.6	274.0	284.6
3.7	72.3	102.9	
1.8	37.9	197.4	
1.8	36.9	366.5	

TABLE 8. Seasonal wood volume increments in red alder saplings expressed as proportional increase

Only 3 year and 4 year olds were analyzed this way since the
other age classes contained very few saplings in the
area sampled

3 YEAR OLD STEMS			4 YEAR OLD STEMS		
Volume after 2 yrs (cu cms)	Volume after 3 yrs (cu cms)	Increment factor	Volume after 3 yrs (cu cms)	Volume after 4 yrs (cu cms)	Increment factor
50.36	54.24	1.07	97.2	250.8	2.58
29.45	123.20	4.18	159.2	322.3	2.02
54.41	181.28	3.33	150.6	698.7	4.63
43.91	217.45	4.95	91.8	195.9	2.13
149.17	812.84	5.44	158.7	674.1	4.24
53.3	148.1	2.77	229.9	631.0	2.74
64.5	320.8	4.97	79.6	345.7	4.34
93.9	210.7	2.24	78.3	289.5	3.69
186.8	405.8	2.17	76.28	165.2	2.16
72.3	102.9	1.42	121.5	324.0	2.67
37.9	194.4	5.20	144.8	333.1	2.30
58.8	498.2	8.47	99.8	397.2	3.97
122.1	361.9	2.96	211.5	654.0	3.09
36.9	366.5	9.93	85.8	338.6	3.95
87.2	301.1	3.45	80.2	320.1	3.99
74.9	237.2	3.16	223.6	375.1	1.67
45.4	103.3	2.27	45.8	146.2	3.19
19.5	97.2	4.98	182.8	471.5	2.58
31.2	159.2	5.10	33.0	82.0	2.48
28.9	150.6	5.21	54.7	36.5	0.66
23.9	91.8	3.84	77.1	198.4	2.57
19.6	158.7	8.09	79.1	144.1	1.82
41.9	229.9	5.48	106.5	153.4	1.44
13.9	79.6	5.72	48.1	136.2	2.83
25.0	78.3	3.13	38.1	80.7	2.11
14.17	76.28	5.38	78.0	250.2	3.20
17.5	121.5	6.94	69.7	118.6	1.70
28.4	144.8	5.09	121.3	314.2	2.59
167.9	608.5	3.62	52.7	76.8	1.45
12.4	99.8	8.04	51.5	105.1	2.05
90.9	319.8	3.51	51.2	105.1	2.05
35.9	211.5	5.89	52.9	94.6	1.78
119.0	310.3	2.60	60.4	219.0	3.62
13.0	85.8	6.60	103.1	168.1	1.63
39.0	198.0	5.1	30.0	75.5	2.51
17.3	80.2	4.63	43.1	74.9	1.73
			18.5	51.3	2.77
33.4	116.7	3.49	26.3	60.0	2.28

TABLE 8. (Cont'd)

3 YEAR OLD STEMS			4 YEAR OLD STEMS		
Volume after 2 yrs (cu cms)	Volume after 3 yrs (cu cms)	Increment factor	Volume after 3 yrs (cu cms)	Volume after 4 yrs (cu cms)	Increment factor
27.3	182.8	6.69	70.3	233.4	3.32
44.8	159.2	3.55	40.1	86.4	2.15
14.4	103.2	7.16			
20.7	124.9	6.03			mean ($\bar{x}$) increment factor = 2.58 S.D=1.04
18.1	54.7	3.02			
44.4	77.1	1.73			
22.8	79.1	3.46			
37.2	106.2	3.86			
15.5	48.1	3.10			
9.8	38.1	3.88			
13.1	78.0	5.95			
20.7	69.7	3.36			
31.9	121.3	3.80			
16.7	52.7	3.19			
16.47	51.5	3.19			
12.1	51.2	4.23			
14.4	52.9	3.67			
9.6	60.4	6.29			
23.8	103.1	4.33			
14.7	70.3	4.78			
10.1	40.1	3.97			
13.4	71.4	5.32			
		mean ($\bar{x}$) increment factor = 5.07 S.D=2.01			