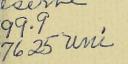
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Differential effects of the

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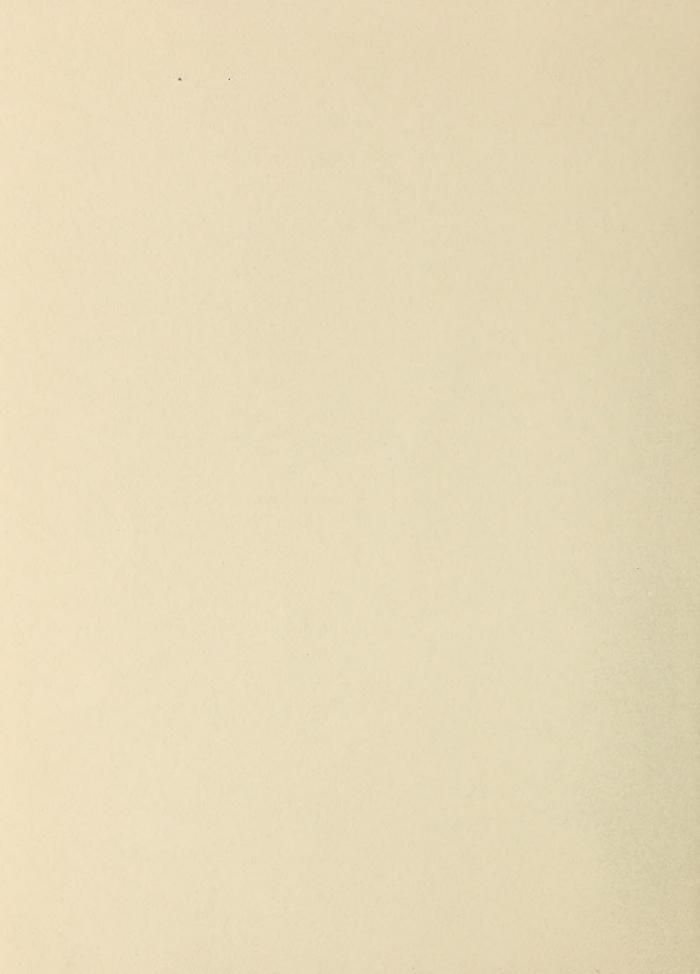
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CURLENT SERIAL RECORDS

PACIFIC NORTHWEST FOREST AND RANGE EXPERIMENT STATION U.S. DEPARTMENT OF AGRICULTURE

BY CARROLL B. WILLIAMS

U. S. FOREST SERVICE RESEARCH PAPER PNW 33



INTRODUCTION

Differential effects of defoliating insects on forest trees are often observed but seldom recorded in a systematic way. The most noticeable differences are usually associated with tree species. This may or may not be the result of larger populations of feeding insects concentrated on these tree species. The population growth of many insect species and the development of individual insects are usually closely synchronized with the development of a particular plant host. This plant host is usually the one most susceptible to attack and subsequent injury.

The spruce budworm (*Choristoneura-fumiferana* (Clem.)) is one of the most important defoliating insect species in Western forests. In these forests, the insect causes the greatest amount of damage to true firs (*Abies* spp.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and Engelmann spruce (*Picea engelmannii* Parry). A different form of the budworm from the one that damages forests with the above species has been reported damaging forests of ponderosa pine (*Pinus ponderosa* Laws.) and lodgepole pine (*Pinus contorta* Dougl.) (Graham 1952, p. 200; Mather 1932).

The larval feeding period commences in spring and ends in midsummer. Larvae issuing from hibernation often mine needles, but the subsequent attack on opening buds and new growth causes the major feeding damage. Once the current year's needles and staminate flowers are destroyed, larvae will feed on older needles.

The general effect of large larval populations is severe defoliation, reduction of the normal vegetative bud complement, topkilling, reduction of annual increment, and, if continued for several years, tree mortality.

This study was made to determine the differences among grand fir (*Abies grandis* (Dougl.) Lindl.), Douglas-fir, and Engelmann spruce tree species in susceptibility to damage by the spruce budworm and, concomitantly, the impact of this damage on the respective competitive abilities of the several host tree species.

Study Areas

The study was conducted in 1958 and 1959 in four forest stands in the Wallowa National Forest of Wallowa County, Oregon, which had been recently heavily infested by budworms for 8 to 12 years. These stands were the primary

 $\frac{1}{1}$ Names and dates in parentheses refer to Literature Cited, p. 16.

infestation centers within the National Forest for the 1944 to 1956 spruce budworm outbreak. This outbreak was not chemically controlled, but by 1956 the budworm populations were no longer causing severe defoliation.

The Wallowa National Forest is wholly in Wallowa County, in the northeastern corner of Oregon. About 55 percent of Wallowa County is forest land, 80 percent of which is classified as commercial. Of this, ponderosa pine comprises 40 percent; Douglas-fir, 28 percent; grand fir-spruce, 17 percent; with western larch (*Larix occidentalis* Nutt.), lodgepole pine, and other species making up the other 15 percent (Bones and Schimel 1960). These tree species are encountered in the Wallowa Mountains in forest stands of several distinctive ecological types.

Grasses and islands of ponderosa pine grow on the basalt soils of the dry lowlands and on the southwestern slopes of the foothills, gradually grading into open stands of ponderosa pine, western larch, and Douglas-fir in areas of more moisture. At the higher elevations following an increasing moisture gradient, the latter species are encountered in mixed stands with grand fir, lodgepole pine, and Engelmann spruce. Spruce and subalpine fir(*Abies lasiocarpa* (Hook.)Nutt.) are abundant near timberline and along banks of streams. Grand fir, subalpine fir, Douglas-fir, and Engelmann spruce make up a large percentage of stands in the principal areas of budworm infestations.

METHODS

In 1958, 2 years after the spruce budworm outbreak had subsided, grand fir, Engelmann spruce, and Douglas-fir trees in the budworm-attacked stands exhibited wide variations in external damage symptoms. These damage symptoms were placed into various groupings to form four damage classes--light, moderate, heavy, and severe intensities of damage--and subsequently were shown to be directly related to the increment reductions occurring in trees exhibiting the symptoms. Radial increment was more responsive than height or volume increment to the various intensities of budworm feeding, supported the greatest number of damage classes, and provided the sharpest delineation among the damage classes. $\frac{2}{}$

Since this study reports the effects of budworm feeding on growth of tree species that appear to be competing for space and nutrients, some description of this competitive appearance is in order. If the branches of adjacent trees were intertwined or nearly touching and if the growth of one tree appeared to

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 $[\]frac{2}{}$ Williams, Carroll B., Jr. The impact of defoliation by the spruce budworm on the growth, specific gravity, and competitive abilities of three tree species in northeastern Oregon. Ph.D. thesis on file Univ. of Michigan library, Ann Arbor, Mich. 213 pp., illus. 1963.

be affecting the growth of its adjacent neighbors, these trees were judged to be in competition and were felled for study. Hereafter in the text, each group of apparently competing trees will be termed a competitive situation. Eleven competitive situations were examined in the study. However, to reduce repetition, the analyses of only eight are presented here.

Each tree in the eight competitive situations was rated by damage class and its diameter at 4.5 feet (d. b. h.) measured. The tree was felled, and six disks were cut at specific internodes along the stem: four were within the crown at the 1951, 1947, 1937, and 1927 internodes; one from the approximate base of the crown; and the sixth from the stump level. Total height, annual height increment (1941-58), and length of dead tops were measured on each felled tree and the number of annual rings were counted on the stump. Descriptions of the study trees and a summarization of their total height data are presented as case histories in table 1. Height increments were also graphically compared within each competitive situation (figs. 1 to 8).

Radial increment was obtained from the disks by measuring the annual ring widths along three radii for each disk, averaging these measurements for each disk, and then combining these to represent the average radial growth per tree. Radial increments made from 1935 to 1958 were graphically compared for trees in each competitive situation (figs. 1 to 8). Although these graphical comparisons are case histories of the trees in each competitive situation, they are believed by the author to illustrate the general observed conditions within the study areas.

RESULTS

The damage ratings shown in table 1 and the graphic portrayal of radial and height increment for eight case histories demonstrate that Douglas-fir was not as severely injured by spruce budworm feeding as other host species. * Figures 1 to 8 show that radial growth of both Douglas-fir and grand fir declined during the early years of the budworm outbreak but that radial growth of Douglasfir recovered during the period 1950-55. Figures 1 to 8 show that, in general, height growth of both species declined in 1949; however, height growth of Douglasfir started an upward trend during 1955-57 but height growth of most grand fir trees continued to decrease. In six of eight competitive situations, grand fir suffered topkilling, three grand firs gradually developed new tops, and on others deterioration of killed tops was progressive.

Differential effects of spruce budworm feeding on these two tree species are thus clearly shown. Whether grand fir is a preferred host, as compared with Douglas-fir, cannot be proven by these data.

Limited information was also obtained on differential effects of budworm feeding on ponderosa pine (fig. 3) and Engelmann spruce (fig. 5). Generally, the growth rate of spruce was reduced more than either ponderosa pine or Douglas-fir.

Table 1.--Case histories for insect-damaged trees involved in each competitive situation.

Wallowa National Forest, 1941-58

Live height, 1958			30.8 43.0	44.0 35.2	46.4 53.0 53.0	30.2 55.0	67.0 88.0 81.0	63.0 76.6 67.6	47.0 57.0	46.0 58.0
Net height growth, 1941-58			10.5 13.4	18.7	11.7 16.0 14.4	0 17.1	0 7.8 9.0	10.8 7.2 8.3	19.1 20.3	16.6 17.8
Length of dead top		Feet	5.2	0 3.8	9.0 0	19.8 0	14.0 0 0	0 8.4 5.5	00	00
Height when topkilling occurred on grand fir			36.0 39.3	40.8 39.0	50.0 48.4 50.7	50.0 46.9	81.0 85.1 76.6	59.0 80.8 72.0	11	11
eight	1958		36.0 43.0	44.0 39.0	50.0 53.0 53.0	50.0 55.0	81.0 88.0 81.0	63.0 85.0 72.0	47.0 57.0	46.0 58.0
Total height	1941		20.3 29.6	25.3	34.7 37.0 38.6	39.9 37.9	71.2 80.2 72.0	52.2 69.4 59.4	27.9	29.4 40.2
D.b.h.		Inches	9.5	9.8 8.8	8.8 14.4 13.0	11.1	14.0 15.8 13.4	10.2 12.0 10.2	9.5	10.1
Age <u>1</u> /	Age <u>1</u> /		62 71	61 66	70 71 74	55	112 135 140	125 128 110	68 62	64 65
Damage description			Heavy Light	Light Moderate	Heavy Light Light	Severe Light	Heavy Moderate Light	Light Severe Severe	Light Light	Light Light
Damage class			III	II	I I I I	IV I	I II II	I U IV	нн	п
Tree species			Grand fir Douglas-fir	Douglas-fir Grand fir	Grand fir Douglas-fir Ponderosa pine	Grand fir Douglas-fir	Grand fir Engelmann spruce Douglas-fir	Douglas-fir Grand fir Grand fir	Douglas-fir Grand fir	Douglas-fir Grand fir
Case history			1	2	m	4	2	9	7	œ

 $\frac{1}{2}$ Stump level.

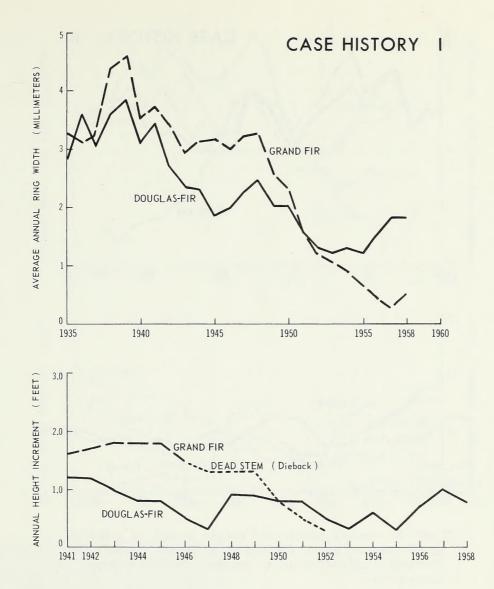




Figure 1.--Annual increment comparisons and photograph of a heavily damaged grand fir and an adjacent, lightly damaged Douglas-fir which appeared to be competing with each other. The grand fir had the higher growth rate and was rapidly overtaking the Douglas-fir until feedings by spruce budworm killed its top and reduced its growth rate more than that of the Douglas-fir.

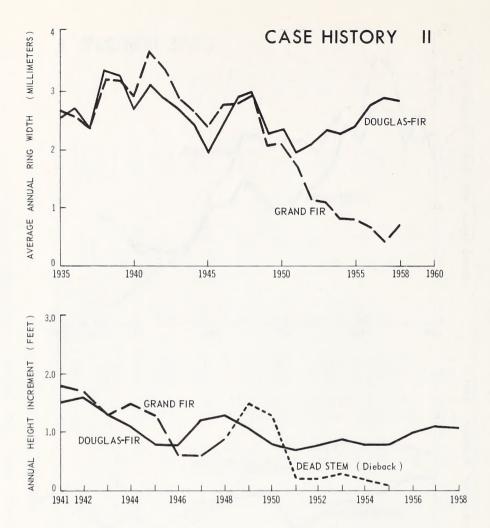


Figure 2.--Annual radial and height growth of a moderately damaged grand fir and an adjacent, lightly damaged Douglas-fir which appeared to be in sharp competition.





Figure 3.--Annual radial and height growth comparisons and photograph of a heavily damaged grand fir tree and adjacent, lightly damaged Douglas-fir and ponderosa pine trees which appeared in competition for available space, moisture, and nutrients. The grand fir grew more vigorously than its neighbors during the predamage period, but its growth rate was affected most by defoliation. The growth of the pine was intermediately affected, and that of the Douglas-fir least affected by defoliation.

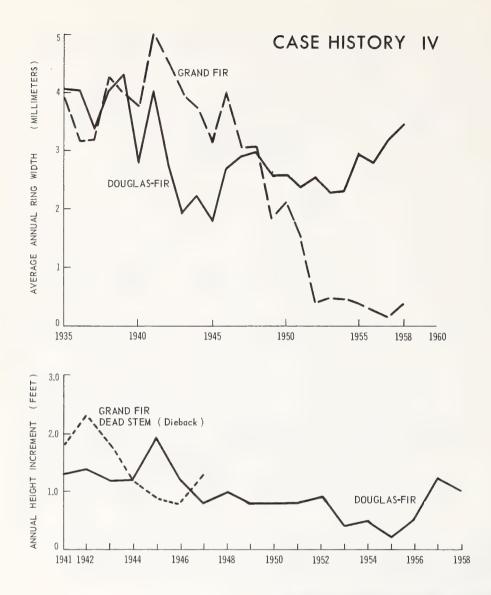


Figure 4.--Annual radial and height increment comparisons and photograph of severely damaged grand fir and adjacent, lightly damaged Douglasfir trees. These trees appeared to be competing until 1947, when the top of the grand fir was killed by budworm feeding. The following year, the grand fir's radial increment was less than that of the Douglas-fir and remained at a very low level. In the summer of 1958, when the photograph was taken, the once very vigorous grand fir was dying.



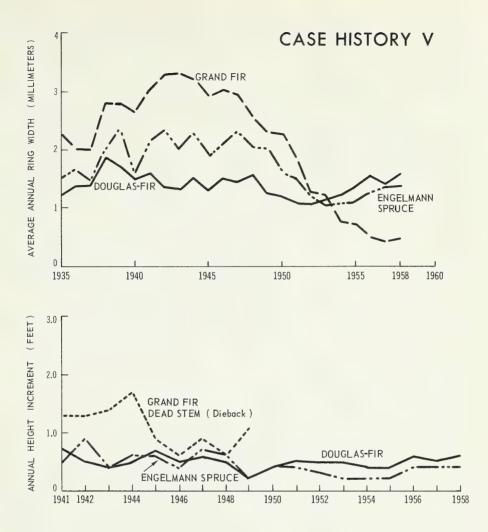


Figure 5.--Average annual height and radial increment comparisons of adjacent heavily damaged grand fir, a moderately damaged Engelmann spruce, and a lightly damaged Douglas-fir tree.

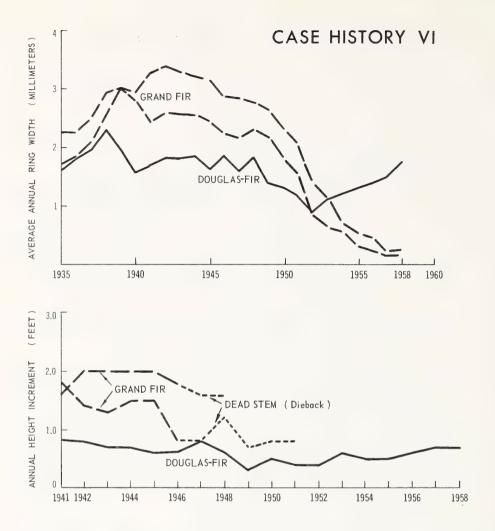


Figure 5.--Annual radial and height growth comparisons of two severely damaged grand fir trees and an adjacent, lightly damaged Douglas-fir tree which appeared to be in competition.





Figure 7.--Annual radial and height increment comparisons and photograph of lightly damaged grand fir and adjacent Douglas-fir trees which appeared in competition. The grand fir grew faster until defoliation reduced its rate of increment below that of the Douglas-fir. In 1958, the radial increment of the grand fir again surpassed that of the Douglas-fir, although height growth still lagged.



Figure 8.--Annual radial and height increment comparisons between lightly damaged Douglas-fir and adjacent grand fir trees which appeared to be in competition.

DISC USSION

Effect of Defoliation on Host Species Competition

On the study areas, damage from defoliation by the spruce budworm was most severe and most variable on grand fir, intermediate on Engelmann spruce, and least on Douglas-fir and ponderosa pine. Grand fir was the fastest growing tree in each competitive situation prior to the budworm outbreak and was consistently damaged more than other competing species. This indicates that budworm feeding populations may be greater on grand fir than on other species and/or similar populations may do more damage to grand fir.

A study made in eastern Oregon by the U.S. Forest Service (1960) showed that similar larval populations caused heavier defoliation and greater budkilling on white (grand) fir than on Douglas-fir. Also, larval survival was found to be higher on white fir than on Douglas-fir. Thus, grand fir is not only more susceptible but also appears to provide more food and/or protection for budworm larvae.

One of the reasons for drastic reduction in the competitive position of grand fir was the high incidence of topkilling that occurred within the species as a result of defoliation. A possible explanation for this is differences in vertical distribution of budworm populations between tree species. In eastern Oregon, median budworm populations were found in the middle third of the crown of grand fir, as in Douglas-fir; however, compared with Douglas-fir, egg masses were more numerous in the upper crown of grand firs and less numerous in the lower crowns (U.S. Forest Service 1961). High populations in the area of the crown, which contained the smallest vegetative bud and foliage complements, logically would be important. This difference in vertical distribution of budworm population occurred between species during the time (1959-60) when populations were low. It appears that a high degree of damage in the upper areas of crowns will result when populations increase and the amount of available food is drastically reduced.

The importance of this difference between tree species in budworm population distribution among crown thirds is accentuated when one realizes that the smaller foliage complement of the upper crown contains a high proportion of the current year's leaves. Since this age group is consumed by budworm larvae before other age groups, the difference in population distribution may explain the heavy top defoliation and topkilling exhibited by many grand fir trees in the areas studied.

Engelmann spruce exhibited the second widest damage variations in the areas studied. In general, these trees were much older, larger, and slower growing than the other species. Their recovery was slower. Ponderosa pine exhibited few external signs of damage and its growth rate was only slightly reduced.

Douglas-fir increment was adversely affected by budworm defoliation, but never to the extent of the associated species. Thus, its relative competitive position was improved. In many cases, Douglas-fir increment increased after initially declining in response to defoliation; on adjacent grand fir or Engelmann spruce, growth continued to decline.

Douglas-fir trees may have the ability to sustain heavy defoliation and remain alive. Silver (1960), describing an outbreak by the spruce budworm in British Columbia, reported that numerous trees had all buds killed and lost over 90 percent of their foliage. However, no tree mortality occurred. Topkilling was common but usually affected only a few years of terminal growth. However, the outbreak lasted only 6 years, and no locality was subjected to more than 2 years of continuous severe defoliation.

The author has observed young shoots on Douglas-firs still elongating several weeks after the completion of budworm larval development. The new leaves produced on these elongating shoots escape injury by spruce budworm larvae for the season. Consequently, Douglas-fir would be affected less by spruce budworm defoliation than the true firs whose seasonal shoot elongation is completed earlier.



Understory in most stands damaged by defoliation was predominantly grand fir. In several locations, many of these young trees were almost stripped of foliage, and in others they appeared to be hardly touched by the spruce budworm. After the budworm outbreak subsided, many of these trees recovered rapidly from the effects of defoliation and in a few years regained favorable competitive positions relative to adjacent associate species (fig. 9). Many grand fir laterals, which had turned up to become leaders, exhibited vigorous height growth, often exceeding the normal leader height growth of less budworm-susceptible species.

Figure 9.--A young grand fir adjacent to a young ponderosa pine. The grand fir's top was killed during the damage period, but after the budworm outbreak subsided, two new leaders were formed and grew vigorously, quickly overtopping the adjacent pine.

Epidemiology

The susceptibility of grand fir to budworm defoliation suggests that the species may be analogous to balsam fir (*Abies balsamea* (L.) Mill.) of Eastern North America in this respect. In the East, spruce budworm outbreaks develop and gain momentum in forests characterized by a high content of mature or overm ture balsam fir spread over large areas (Morris 1958). Increases in budworm populations seem to favor balsam as contrasted to spruce (usually white spruce, *Picea glauca* (Moench) Voss), mature balsam as contrasted to young age classes, dense stocking of balsam as contrasted to open stocking, and extensive areas of balsam as contrasted to isolated stands (Morris 1958).

One thing the study areas in the Wallowa National Forest had in common was a substantial number of grand fir trees. Other areas in eastern Oregon, shown by aerial damage survey maps to have experienced severe defoliation damage, also had grand fir. An examination of the budworm dynamics from 1947 to 1958, mapped by annual aerial surveys, revealed that these areas were the focal points from which the budworm outbreaks spread and to which they eventually withdrew.

The reasons for the relative success of budworm populations on mature and overmature balsam fir appear to be nutritional and phenological. Budworm survival and development are high in balsam fir staminate cones, and mature flowering trees contain heavier budworm populations than nonflowering trees (Blais 1952). Mature flowering trees are usually the dominant ones in the stand, and they are the ones preferred by ovipositing females (Morris 1955). Overwintering budworm larvae emerge contemporaneously with the expansion of balsam fir vegetative buds and are provided with suitable food at the right time (Graham 1952, p. 201).

A study of spruce budworm development under field conditions in eastern Oregon reported that budworm larval growth and development was related to the growth of grand fir (Wagg 1958). If the growth variation between trees in dense stands and those in open stands was considered, it was possible to estimate budworm larval development from the amount of grand fir lateral stem growth. This suggests that budworm development in the Pacific Northwest is related to the development of the current year's grand fir foliage--a phenological event analogous to that of balsam fir and the budworm in the Northeastern States. Blais, J. R. 1952. The relationship of the spruce budworm (*Choristoneura fumiferana* Clem.) to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.). Can. J. Zool. 30:1-29, illus.

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worm outbreak in eastern Oregon. U.S. Forest Serv. Res. Pap. PNW-33, 16 pp., illus. Pacific Northwest Forest & Range Experiment Station, Portland, Oregon. Generally, defoliation reduced growth of all eastern Oregon conifers subjected to the 1944-56 spruce budworm outbreak. Grand fir, the most vigorous before the outbreak, suffered most; Engelmann spruce was intermediately affected; and Douglas-fir and ponderosa pine were least affected. Growth of less injured species declined slower than adjacent grand firs and, after initial decline, often improved in direct proportion to continued decline of grand firs. Severity of defoliation was the determining factor in subsequent growth recovery.

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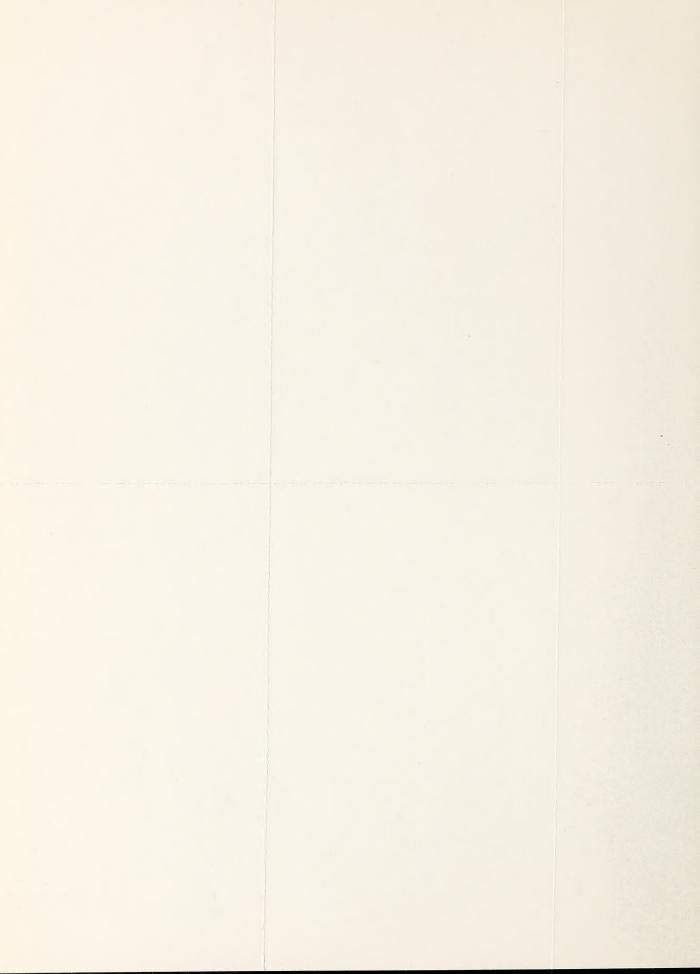
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