PHYTOECOLOGICAL IMPACTS AND MANAGEMENT IMPLICATIONS OF

THE DOUGLAS-FIR TUSSOCK MOTH

NEAR KAMLOOPS, BRITISH COLUMBIA

by

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ABSTRACT

Seven outbreaks of Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough, have recurred in the interior of British Columbia since 1915. But little is known about their impacts on renewable resources in affected stands. A study was undertaken to examine effects of the most recent outbreak on understory vegetation and tree productivity near Kamloops, British Columbia.

Dry weight forage production was sampled from $1m^2$ circular plots under various levels of stand crown cover (0-96%) and density (0-45.9m^2/ha), as modified by defoliation. Crown cover was determined using a moosehorn, and from vertical photographs obtained with a 160° lens mounted on a conventional camera. Stand density was determined using a 20 factor prism. Increment cores were obtained at breast height, and radial growth analysed under the Addo-X. Ring width behaviour was compared with occurrence of past outbreaks. The ecological literature on *O. pseudotsugata* was reviewed.

Negligible amounts of forage were obtained from many plots with undefoliated trees. In defoliated plots with live trees, total forage production ranged from 0.0 under 96% crown cover and 45.9 m^2/ha density to 648.9 kg/ha under 50% crown cover and 16.0 m^2/ha density. The average yield in small openings was 3667.4 kg/ha. High variability was evident. In one stand, two years following its defoliation and consequent death, total forage yields exceeded those from nearby small openings. Forage yield data were described better by logarithmic models

than by hyperbolic ones, at 95% probability. Impacts on tree growth
were not demonstrable one year following defoliation. Many trees
recovered even from complete defoliation. Insect outbreaks and periods
of slow tree growth coincided, but quite inconsistently. Apparently,
most scattered infestation patches develop independently of each other.

Grazing values should increase in seriously defoliated stands
even without range seeding. On poor sites and in stands managed
primarily for forage production, outbreaks of *O. pseudotsugata* may be
left alone without necessarily endangering remote stands. Selective
control favoring better sites managed for tree production should improve
efficiency of investing scarce funds in protection of the inventory.
Tree growth and insect outbreaks may be under the influence of some
regional climatic factor, but local factors are also important. A need
remains for long term impact studies on tree growth, forage yield and
nutrient status, and other resources.

ACKNOWLEDGEMENTS

I should also thank all the loggers, ranchers and graziers I met and talked to in the field, for telling me some of their experiences in the specific study area.

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In the past, we have often worked on the premise that all insect and disease outbreaks are detrimental and must be controlled. Perhaps in most instances this has been true, but the effect of the outbreak on wildlife and aesthetic resources may have been a positive factor that needs more recognition.

A justification for Federal funds must now be very carefully considered and prepared. The President's Office of Management and Budget is not particularly impressed by the general statement that millions of acres of trees are infested by insects and that a large volume of timber is dying. Nor is it impressed that many livelihoods are tied directly to the forest resource or with similar arguments. What does impress the office are specific benefits that can be derived from the expenditure of alternative amounts of Federal dollars. In other words, the benefit-cost evaluation is directly associated with the proposed project. We must never forget that every dollar appropriated for forest insect and disease protection is one less dollar available for medical research, mass transit, flood relief assistance or similar needs.

We must be in a position to point out what effects are specifically associated with forest pests or pollutants when no corrective action is taken. And we must be able to quantify the benefits that will acrue ... under alternative levels of spending for forest pest management and environmental quality evaluation activities. When we have good information, we can make good decisions ....

The value of general estimates for analytical purposes is small. We need reliable comprehensive data of forest insect and disease losses (and benefits) that will stand up to close scrutiny. If this information were now available we could evaluate our losses more realistically and use scarce funds and manpower more efficiently ....

John R. McGuire, Chief, U.S. Forest Service. At the 1974 Symposium on the Spruce budworm, Alexandria, Virginia.

INTRODUCTION

The latest outbreak of Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough (Lepidoptera: Liparidae), in the interior of British Columbia is the most devastating of all seven recorded outbreaks which have recurred there since about 1915. Outbreaks have occurred quasi-synchronously over a wide geographic region in western North America. They also occur quite regularly with a mode of about eight years between outbreaks in many places in southern British Columbia (Fig. 1).

Outbreaks are confined to the interior Douglas-fir[1] forest, specifically to the ecotone between lower elevation Ponderosa pine and higher elevation Douglas-fir types. Critical synecological data for zonal ecotones here are lacking (Tisdale and McLean, 1957) even now. Because plants continually contend with each other in the tension zone, there is no stable association in the strict sense of the term. Notwithstanding, an edaphoclimatic "climax" association may be defined here as Douglas-fir-Ponderosa pine-Blue bunch wheatgrass, for purposes of this thesis.

No region in the province has more renewable natural resource values and uses converging upon the forest than the southern interior. Critical values include timber, fish, range and forage for wild as well as domestic ungulates, aesthetics, soil and watershed. Inasmuch as various sectors of the public make overlapping demands on the resources within an ecosystem, conflicts exist in their management. Compatibility is possible, but it is not as evident as conflicts. As various

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[1] Scientific names of plants are available in appendix.
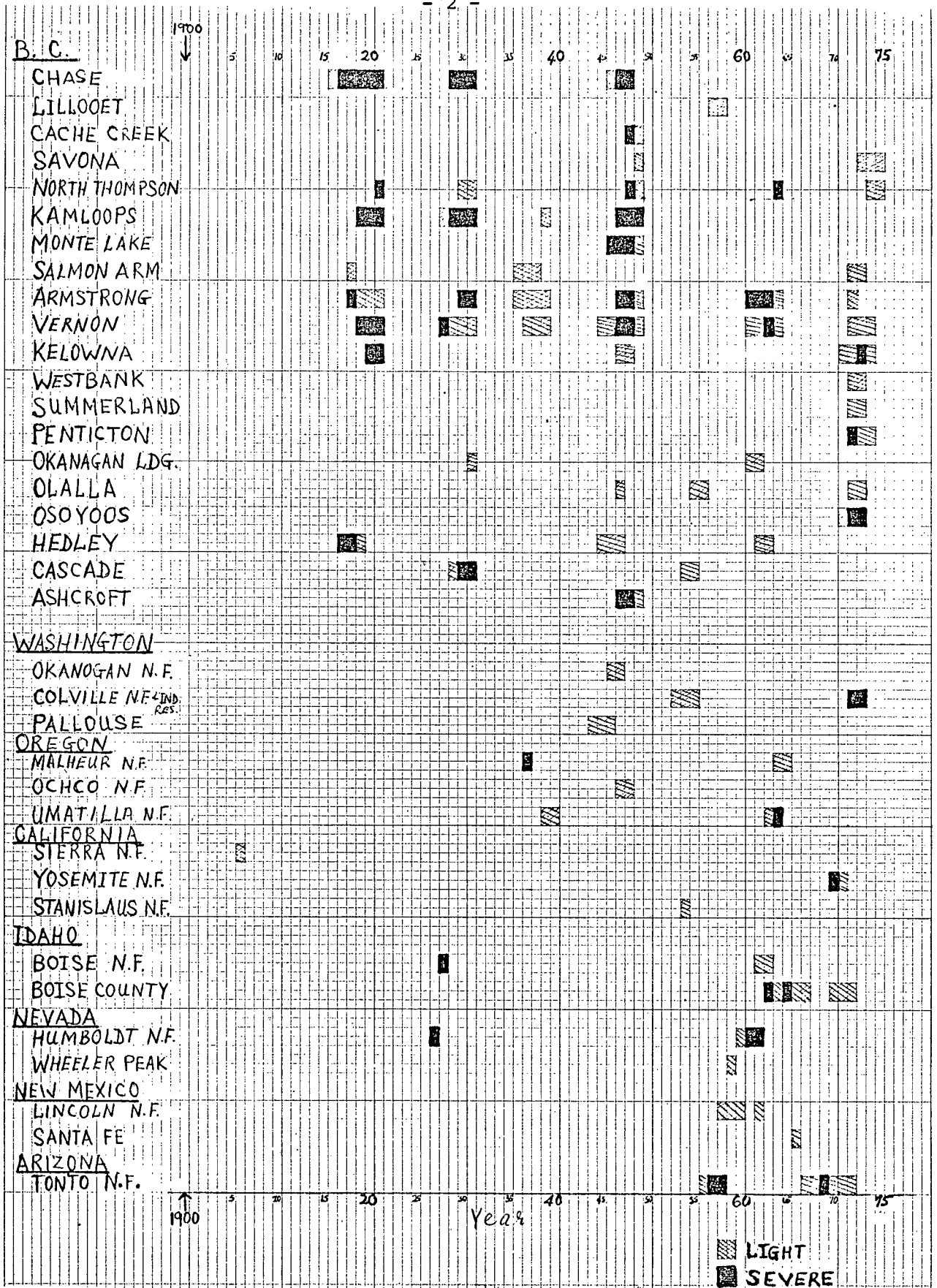
Figure 1. Major outbreaks of Douglas-fir tussock moth in western North America. The chart represents outbreaks recorded in numerous accessible literature. Main sources: Sugden, 1957; Canadian Forestry Service's Forest Insect and Disease Survey reports; U.S.D.A.-U.S.D.I. ... Douglas-fir tussock moth pest management plan, 1973).

resource values converge on an ecosystem, so do their managers and users. Since 1973, when the current outbreak surfaced, concern has been expressed about its impact on the ecosystem. Arguments about the impacts are mainly empirical, and are compartmentalized often with groups promoting polarized views. Some graziers and wildlife managers contend that defoliation is beneficial because it results in increased understory forage yield and quality. Some forest managers, on the other hand, maintain that notwithstanding the low site quality of infested stands, the wood, fiber and watershed values exceed those of other sympatric resources. The problem of resource use becomes more complex as various public interests become involved. Many arguments are based on intuition and empirical evidence. Specific data are lacking. As some arguments are speculative, they may provide questionable ground on which resource management decisions are based. The need for relevant data is obvious. This thesis investigates and reports some real and potential ecological impacts of Douglas-fir tussock moth outbreaks in a part of the Kamloops Forest District, in the British Columbia interior. The data should aid resource managers there in making well-founded decisions regarding outbreaks. The thesis also examines some ecological aspects of the insect, and discusses a rational approach towards a strategy for its management.

The insect

The Douglas-fir tussock moth is a native of western North America where it is one of the most destructive forest defoliators. It was described by McDunnough (1921) from a holotype or specimen of

several paratypes from Chase, B.C. It was he who separated the insect

from *Hemerocampa vetusta gulosa* complex. In the American literature,

the insect is still sometimes referred to as *Hemerocampa pseudotsugata*

(Grant et al., 1975; Harwood, 1975). In Canada, the genus *Orgyia*

appears to have been completely accepted since about 1961.

The life cycle of the insect varies along ecoclines within

its wide geographic habitat. Adults emerge, mate and lay eggs within a

short period in summer. The eggs, in diapause, remain unhatched

throughout the winter. Larvae emerge in spring and begin feeding in

the upper and outer parts of tree crowns. The larvae trek to those

parts immediately following emergence. The apparent photopositive

reaction is possibly triggered by hunger (tension) as in Eastern spruce

budworm, *Choristoneura fumiferana* (Wellington, 1948). In the European

Orgyia antiqua the photopositive reaction is inhibited by some tactile

sensors in the forelegs: at the end of a branch, absence of tactile

stimuli leads larvae to revert to exploratory maneuver (Zanforlin,

1970) so that the insect does not fall off. Five larval instars – ♂♂

may have one less – are most common. Although as many as seven instars

have been mentioned (U.S.D.A., 1973b), this has not been ascertained

in the scientific literature.[2] Sexual dimorphism of non-sexual

characteristics is exhibited by adult Douglas-fir tussock moths: ♂♂

have normal lepidopterous wings, and ♀♀ nonfunctional vestigial ones.

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[2] It is well known that rearing insects on low quality food may increase
the number of larval moults (Leonard, 1970). To what extent the
endocrine system – corpora allata, ecdysial glands – is influenced
by the food is not clear.

Host "preference" also varies by region. In B.C., Douglas-fir is the preferred host; sympatric trees such as Ponderosa pine are rarely attacked. The preference for Douglas-fir was implied by McDunnough (1921) in his classical paper where he reported some rearing results. The preference is evident also from Forest Insect and Disease Survey records, and field observations. In the U.S. Pacific Northwest, White fir and Grand fir are preferred, but Douglas-fir is often attacked (Eaton and Struble, 1957). Other hosts there and farther south include Western larch, Western hemlock, Subalpine fir and Engelmann spruce (Balch, 1932; U.S.D.A., 1973b). The insect also feeds on lesser vegetation especially when tree foliage is depleted. Beckwith (1976) points out that whether the variation in host preference reflects biological races of the insect is not known.

Ecological impacts

Ecological impacts can be evaluated by assessment at three stages in the sequence of events: before, during and following application of the ecological force. Potential impacts are evaluated before the activity. In the U.S., this is often done as a necessary part of environmental project feasibility analysis under the 1960 Federal National Environmental Policy Act Section 102. The resulting Environmental Impact Statements attempt to predict outcomes of socioecological significance. The U.S. Forest Service has already undertaken impact studies for a few forest insects including the Douglas-fir tussock moth. The voluminous 1973 Draft Environmental Impact Statement for the tussock moth (U.S.D.A., 1973b) in the Pacific Northwest

centered on whether and how the insect should be controlled. A benefit-cost ratio of 13 (D.A. Graham, 1974) clearly justified control. However, it was difficult to decide on how to control the insect because, as Harwood (1975) pointed out, after a survey of the literature Stark found very few "scientific papers" on this insect pest.

Impacts and their magnitudes vary with intensity, frequency, severity and timing of the respective ecological force. Impacts are also a function of the ecosystem prevalent when the force is applied.

Figure 2 illustrates possible relationships between many factors involved in determining the impact of an outbreak of Douglas-fir tussock moth. The model becomes more complex when a management decision is superimposed on the system. Some of the relationships are hypothetical, but they should be appreciated by decision makers and resource managers involved in the problem.

The tussock moth directly affects various parts of the vegetation. This, in turn, affects the stand of which secondary vegetation may be a major component. The extent to which impacts are evident at various levels of stand, forest etc. in the hierarchy depends mainly on the spatial or geographic extent of an infestation. Reciprocal impacts are real: I infer from data presented by Condrashoff and Grant (1962) that depletion of tree foliage results in a change of preference for oviposition and diapause to parts of trees nearer to the ground, where predation may be intense. Weather, elevation and other external factors also influence impacts of defoliation.

As the model indicates, there is an impact at any level in the hierarchy. For a small outbreak, a pest management decision may
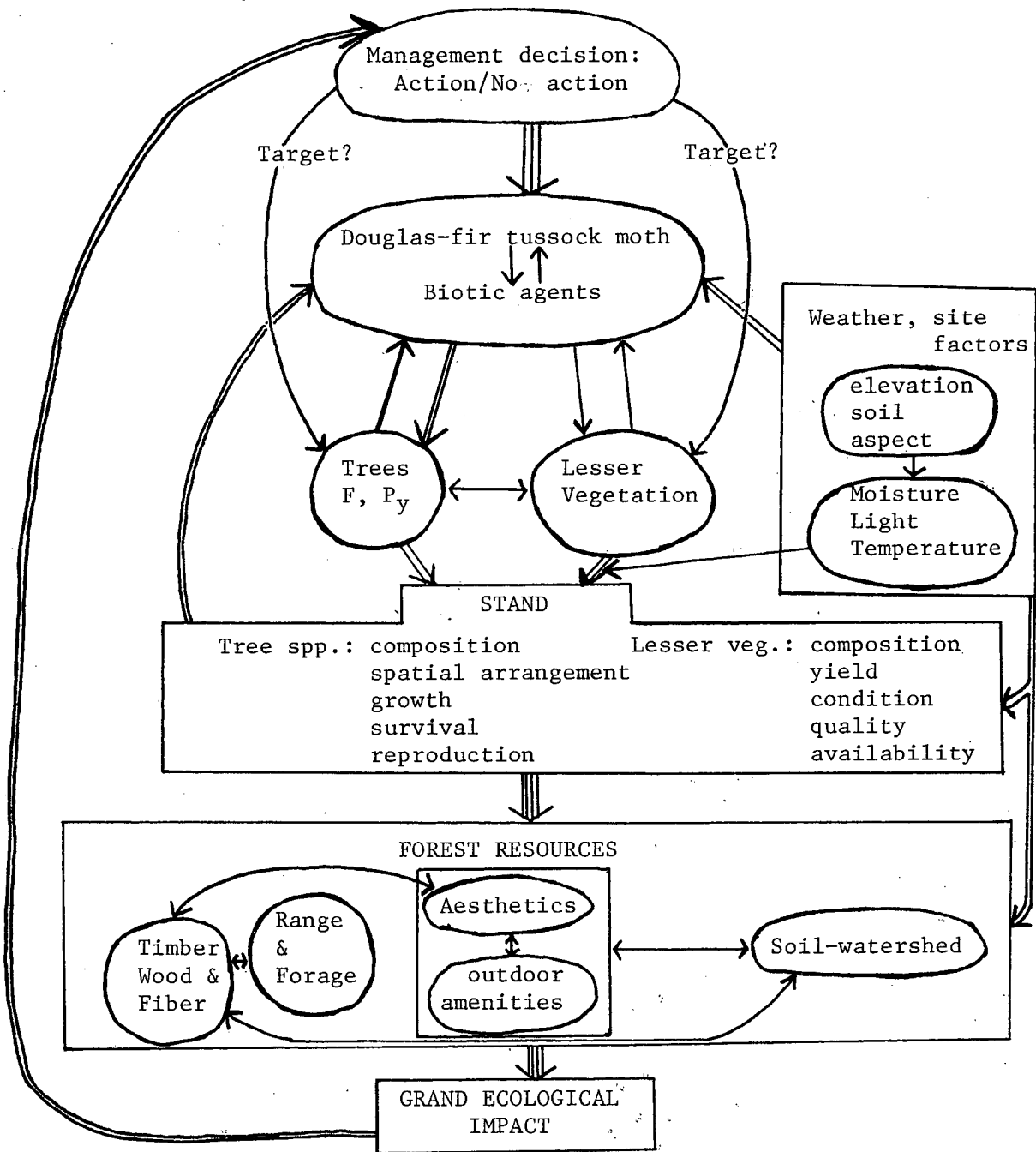
Figure 2. A model of interrelationships between important factors interacting in an outbreak of Douglas-fir tussock moth. Arrows indicate flow of influence; thickness of arrows indicates relative intensity or importance of influence. NOTE reciprocal impacts e.g. Trees→Douglas-fir tussock moth.

probably be based on impacts at the stand level. For extensive outbreaks, however, it is necessary that decisions be made following analyses of impacts on resources at the regional level. Such analyses should provide the rationale or raison d'etre and its basis for the fundamental decision of control or no-control.

Until recently most ecological impact analyses were pre-occupied with evaluating effects of (chemical) control decisions, often bypassing the direct ecological impacts of the insect itself. It was often assumed a priori that damage was serious enough to warrant some control. Furthermore, emphasis was on investigations of effects on the animal community, mainly birds, fish and ungulates. Insects were examined in followup studies by entomologists to determine efficacy of the control measures. Apparently, the long time it takes for impacts to show in some parts of the ecosystem discouraged serious research there. Thus, impacts on the plant community have largely been ignored in Douglas-fir tussock moth outbreaks. In this thesis I emphasize impacts on the phytocoenose - the tree and lesser vegetation. Even within this restriction, for practical reasons, the need for evaluating only the more important impacts is evident. Other impacts are not ignored, however.

The study area

The study area is in what is generally referred to as the North Thompson and Kamloops in Forest Insect and Disease Survey reports. It is tdominated by unevenaged, mostly second growth Douglas-fir-Ponderosa pine stands.

The interior is a part of the Dry Forest Biotic Area which is
"faunistically most closely related to, and indeed forms a northern
extension of the Great Basin Complex" (Munro and McT. Cowan, 1947). No
detailed synecological studies relevant for the outbreak zonal ecotones
are available in the accessible literature. Broadly, the area is a
part of Rowe's (1972) M-1 or Ponderosa pine Douglas-fir section of the
Montane Forest Region, and Krajina's (1959, 1965) Interior Douglas-fir
Biogeoclimatic Zone, Dry or Pinegrass subzone. It approximates
Beal's (1974) *Pseudotsuga Agropyron Spicatum* association - "a
topoedaphic climax since both topography and soil are necessary for its
establishment" - of the wetter Southern Cariboo Zone. In the
Similkameen valley, the broad *Pseudotsuga menziesii* zone (McLean, 1969)
embraces ecological conditions common in the study area. The ecotone
does not exactly fit in any of Brayshaw's (1965) distinct associations:
It lies between his *Pinus ponderosa - Agropyron Spicatum* var. *inerme*
and *Pseudotsuga menziesii - Agropyron spicatum* associations. I consider
the zonal ecotone as *Pseudotsuga menziesii - Pinus ponderosae -
Agropyron spicatum* quasi-association, which represents a dynamic
situation and is not truly climax.

Study plots were restricted to the southern part of the North
Thompson Valley near Dairy and Heffley creeks, and Mountain View, and
to the south of Kamloops Lake near Cherry Creek and Indian Gardens
(Figure 3 - folded inside back cover). *Calamagrostis rubescens* was a
minor part of the vegetation in a few plots. Other lesser vegetation
included Balsam root, Timber milk-vetch, Junegrass, Sagebrush, Needle-
and-thread, and Kentucky bluegrass. Most of these plants are

invaders on overgrazed sites. In most plots, soils were generally deep, fine to medium textured. A description of each stand follows.

Cherry Creek - 1974: This stand was severely defoliated in 1974.[3] Plots were located between 653 and 720 m elevation, and between 3 and 25 percent slope. Northeast facing slopes are dominant. The soil is deep, sandy loam. The forest floor depth averaged 3.3cm; in a few plots it was as deep as 7.6cm. Two years following defoliation, twenty three percent of trees tallied had been or was infested with bark beetles. The smallest tree infested had a breast height diameter of 7.9cm. Only one Ponderosa pine tree was infested. Cattle and horses were grazing in the area at the time of sampling. Plots for understory vegetation were, however, located where visual evidence indicated no grazing activity. (Figure 4).

Cherry Creek - 1975: This stand was defoliated in 1975. Plots were located between 683 and 720m, and between 3 and 25 percent elevation and slope respectively. It is generally similar to Cherry Creek - 1974. (Figure 5).

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[3] Information of years when experimental stands were defoliated was given by Dr. R.F. Shepherd, Canadian Forestry Service, Victoria, B.C.

Figure 4.   A fisheye view of a part of Cherry Creek - 1974.

Figure 5.   Cherry Creek - 1975.

Indian Gardens: This is a dry site. The soil is loamy clay with a few rock outcrops scattered throughout. The duff layer averaged 2.5cm in depth. The stand approximates a pure Douglas-fir type as no Ponderosa pine trees were tallied in the sample plots. Plots were within 827 - 921m and 15 to 25 percent ranges of elevation and slope respectively. (Figure 6).

Figure 6. Typical Indian Gardens country.

Mountain View: One stand sampled here was defoliated in 1975. The soil is loamy clay. Plots were located between 518 and 636m, and between 5 and 20 percent elevation and slope respectively. The stand is on a southeast facing slope. Some plots were located in another stand which was defoliated in 1974. Virtually all trees were dead at time of sampling, two years later. A slope of 35 percent was quite common; elevation ranged from 647 and 671m. (Figure 7).

Figure 7. A part of Mountain View.

Dairy Creek: The stand is characterized by deep loamy clay soil, and a forest floor averaging 6.4cm deep. In many plots the forest floor was severely cracked, indicating extreme dryness. Part of the stand was fenced off from grazing for the second consecutive year. The stand faces south. Elevation and slopes of plots were between 624 and 878m, and 5 and 20 percent respectively. (Figure 8).

Figure 8. A representative fisheye view of Dairy Creek.

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Figure 9. Heffley Creek.   Top: hillside

                               Bottom: roadside

Heffley Creek: Two stands both along the creek were sampled here. One stand on the north side of the creek was only lightly defoliated in 1975. Elevation of 588m and slope of 20 percent were typical. The other stand is on the south side on a very steep hillside. I refer to these stands as Heffley Creek - roadside and hillside. The soil is very deep sandy loam. On the hillside, a steep slope of 88 percent makes the soil prone to mass wasting; deep ravines are common here. Probably the angle of repose is not much less than the prevailing 42°. Depth of the forest floor averaged 7.6cm. Bunchgrass is exceptionally dense here. The tussock moth swept through this stand in 1975 and left virtually all Douglas-fir trees completely defoliated. (Figure 9).

Methods

Understory vegetation

In the literature it is evident that forage (= herbage) yield on forested range land is a function of interacting ecological factors. In this thesis I studied the influence of stand density and stocking as modified by defoliation, on understory forage productivity. In each location, temporary plots were chosen in a maximum of six groups of trees representing different ecological conditions:-

No defoliation - high density, low density;

Partial defoliation - high density, low density;

Complete defoliation - high density, low density.

Defoliation classes here refer to the patch rather than individual trees, and the terms high and low density are relative.

For each plot and adjacent area in the stand, I noted stand type, aspect, slope, elevation, soils and the forest association. The purpose was to define part of the ecological domain within which the data would be valid. All plots reported here were within the ranges of 517 to 921m and 3 to 88 percent for elevation and slope.

From each plot center, a sweep was made with a prism of basal area factor 20, to obtain the number of "in" trees. The patch density was determined using principles of variable plot sampling (Dilworth and Bell, 1972). I tallied all "in" trees taller than 1.4m or breast height and recorded the species, breast height diameter (dbh), height, whether it was live, dead or undetermined, recovery potential if defoliated, and presence or absence of secondary insects. For every crown I recorded the following: width, total length, length of dead portion or top kill, and of partially defoliated, and undefoliated sections. The proportion of current year foliage was estimated ocularly. This was possible because of clear distinction in color and position of current and older foliage.

In the past, the use of 9.6 ft^2 microplots was traditional among American range ecologists. Its origin dates back to 1949 when it was proposed independently by Frischknecht and Plummer, and Campbell and Cassady. The rationale was that biomass from the plot in grams is equivalent to one tenth of yield in pounds expected from one acre, or 43560 ft^2. Later, Canadians adopted the same plot size so they could quickly judge the capability of their range land by comparing with American data. Currently, $1m^2$ plots are used with increasing frequency in forage productivity studies. Grams of biomass from a $1m^2$ plot are

equivalent to one tenth of yield in conventional kilograms-per-hectare

units.

Within each tree plot I systematically established four-$1m^2$

microplots. Circular plots have the smallest perimeter per unit area

(Van Dyne et al., 1963), and this minimizes edge effects which may

bias results in forage yield studies. I used a metal loop to determine

microplot boundary:
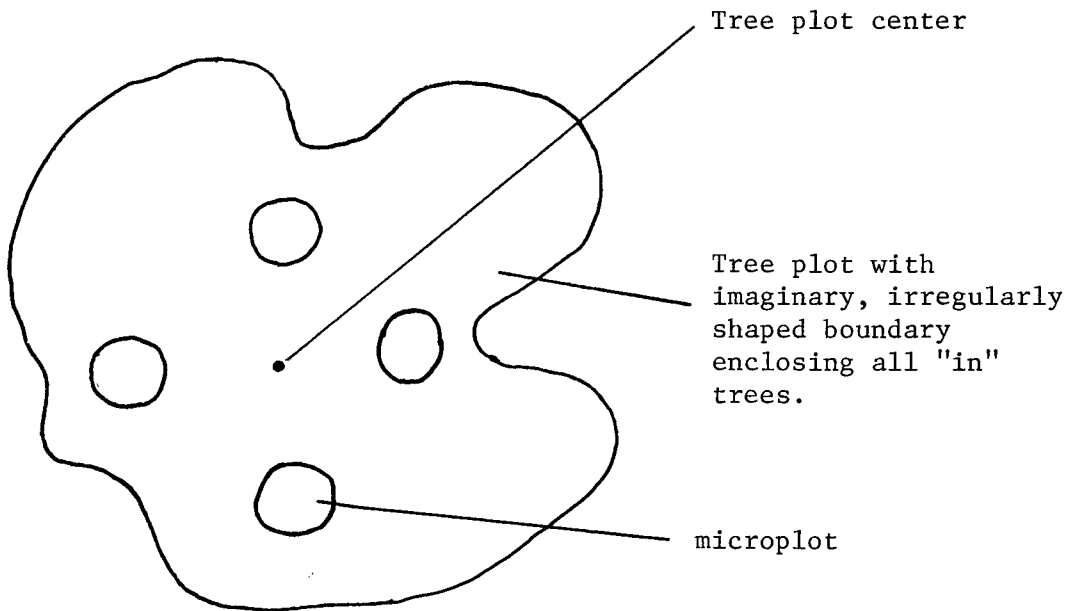
Microplots were established also in openings.

In each microplot a field assistant and I clipped all lesser

vegetation - shrubs, forbs, grasses - rooted within the plot, at root

collar. Tree seedlings were counted but not clipped. The three

components of understory vegetation were separated in the field, put in

bags and later stored in a cold room. The vegetation was then dried at

50°C for 50 hours, and weighed to the nearest one hundredth of a gram

in the laboratory. We did this part of the field work during the summer of 1976.

We estimated crown cover under each plot in two ways. One reading was obtained from above the center of each microplot using a moosehorn invented by Robinson (1947) and later described by Garrison (1949). For reliable and precise moosehorn crown cover estimates, as many as forty readings per one quarter acre plot are recommended (Robinson, 1947; Bonnor, 1968). Our readings fall within this acceptable limit. In spite of difficulties involved in holding the moosehorn vertically and steadily, especially in adverse weather conditions in the field, we found the technique quite precise (Table 1).

Table 1

Ecological conditions prevalent in tree plots where understory vegetation was clipped. Data for crown cover are based on 172 microplots, and for basal area on 36 tree plots.

| | Percent crown cover | | Basal area (m^2/ha) |
	moosehorn	wide angle lens	
Mean	50.10	50.90	21.09
Minimum	0.00	0.00	0.00
Maximum	96.00	90.00	45.90
Stand. deviat.	28.80	25.70	12.20
Coef. of Var.	0.58	0.51	0.58

The second technique involved the use of hemispherical or "fisheye" (160°) lens mounted on a conventional Pentax camera (Brown and Worley, 1965; Bonnor, 1967), loaded with a high speed color slide film. I took crown photographs of each tree plot from ground level, and determined crown closure from prints using a dot grid. This technique requires clear skies, calm weather and some familiarity with photography. It becomes very expensive if the field should be revisited to take more photographs so spoiled ones may be replaced. But it provides a semi-permanent record of the plots. The risk of a film developer losing or even mixing up good photographs is always present. Therefore, plots should be marked, albeit temporarily, and films developed as quickly as possible so that plots can be revisited quickly without difficulty if required. The use of a fixed angle lens in this technique gives crowns of taller trees a better chance of being included in a photograph. Yet it is recognized that shorter trees may have a shading influence of their own. This probably biases estimates of crown cover in uneven aged stands, especially if the angle is narrow and tree plots large. In this study, most tree crowns appeared in the photographs, as in each patch variation in tree height was small.

Tree growth, survival and salvaging.

To investigate possible association between occurrence of outbreaks and trends in tree radial growth, and effects of the tussock moth on tree survival, we obtained increment cores from trees in each tree plot. We cored two Douglas-fir trees - one tree of average dbh, the other of maximum dbh, and two Ponderosa pine trees both of average

dbh. One of the Ponderosa pine trees was from inside, and the other outside the plot. The number of increment cores obtained in each plot was variable as some plots did not have any Ponderosa pine trees, and some trees outside one plot also served for another adjacent plot. Increment cores were preserved in plastic straws; later I analysed them for earlywood, latewood width using the Swedish Tree Ring Machine, the Addo-X. Only two of 229 cores were discarded because of serious defect of rot at a pitch pocket. The freezing technique (Francis et al., 1972) used to detect rings, in rot pockets is valid for studies involving only ring counts for age and site index determination. The technique is inappropriate for studying ring behaviour because in situ moisture may cause changes in cell width. For each Ponderosa pine tree outside the plot, we recorded similar parameters as we did for each tree inside the plot.

Because of apparent high variability in tree growth, I suspected that in order to detect reliable impacts on tree radial growth, some intensive sampling of increment cores within one area was necessary. So in addition to the above, I cored 40 trees for ring width behaviour analyses on a medium site at Mountain View. I did this after tree growth had ceased in winter of 1976. I cored two trees from each of the following 20 treatments: Diameter classes (cm): $\leq$ 15.0, 15.1-25.0, 25.1-35.0, >35.0; and for each diameter class the following crown conditions: Ponderosa pine control; Douglas-fir defoliation classes: control, 5-25%, 30-60%, >65%. All the cored trees had been defoliated in 1975; they were live at time of sampling.

The purpose was to examine historical correlations between

Table 2. Extent of sampling for historical radial tree growth, effects of defoliation by Douglas-fir tussock moth on tree growth and understory forage yields. Site quality - B.C. Forest Service: M - medium, L - Low, P - poor.

	Elevation (m)	% Slope	Site quality	Tree plots	Trees tallied Tot.	Trees tallied %F	Trees cored F	Trees cored Py	Cores analysed	Lesser veg. plots (incl. open)
Dairy Creek	624-878	19-26	M-P	6	72	97	12	3	27	28
Cherry Cr. - 1974	653-720	3-25	P-L	6	57	93	12	8	32	28
- 1975	683-778	3-35	P-L	6	67	88	12	7	34	28
Heffley Cr.- Roadside	558	20	M	2	13	100	3	1	7	12
- Hillside	610	88	M-P	3	-	100	-	-	-	16
Mountain View - 1974	617-671	35	M-P	2	20	100	-	-	-	8
- 1975	519-636	5-20	M	7	89	96	12	8	31	32
- Growth response	561-702	5-20	M	-	40	-	32	8	80	-
Indian Gardens	872-921	15-26	P	4	50	100	8	2	18	20
				36	408		91	37	229	172

Table 3. Extent of sampling for Douglas-fir resilience to, and salvage-
ability of stands following defoliation by Douglas-fir tussock
moth.

	Elevation (m)	% Slope	Strip No.	Strip Size(m)	Trees tallied F	Trees tallied Py	Trees dead F	Trees dead Py	Avge Basal area (m²/ha)
Heffley Cr. Hillside (unsalvaged)	610	88	1	8x31	48	-	15	-	-
	610	80	2	12x40	121	3	21	-	-
Heffley Cr. (Balco-Salvage Oper.)	824	5	1	9x214	44	3	2	-	-
	800	10	2	8x92	12	2	2	-	-
	800	10	3	8x122	79	1	31	-	-
	790	25	4	31x61	28	13	6	-	-
(adj. stands unlogged)				Prism plot					
	790	20	1		8	-	1	-	37
	793	25	2		14	-	6	-	32
	793	25	3		12	-	2	-	28
	793	10	4		5	5	-	1	23
	793	32	5		4	4	-	-	41

past outbreaks and tree growth during corresponding periods, and tree growth responses to different intensities of defoliation in 1975. All increment cores were obtained at breast height. Table 2 shows the extent of sampling undertaken in this part of the project.

Remarkable resilience of Douglas-fir following defoliation by the tussock moth in western U.S. was implied in the literature by Caroline and Coulter, (1975). My field observations suggested that mortality of infested trees varied mainly with size and degree of defoliation. Therefore tallies were taken of individual trees in 2 representative strips at Heffley Creek - hillside, where all trees had been completely defoliated in 1975. The strips measured 8 x 31m and 12 x 40m. A total of 172 trees were tallied in both strips. For each tree, we recorded the species, condition, dbh, height, crown width and length, recovery potential (subjectively determined) and absence or presence of secondary insects. Strips were also located in areas where salvage logging had been undertaken. Trees from there were also used in the resilience study. This part of the study, done in summer of 1976, also served for investigating the nature and impact of salvaging infested stands. (Table 3).

Results

The efficiency of a sampling system is often estimated as the reciprocal of the sample variance. The efficiency of system "i" relative to "j" is given by $\sigma_j^2 / \sigma_i^2 \longrightarrow s_j^2 / s_i^2$. When costs of sampling per unit are not equal, efficiency is modified to $1/[C \times CV^2]$ (Freese, 1962) where C = sampling cost per unit, CV = coefficient of variation.

In this study, one film exposure cost on the average $0.15 for purchase, $0.12 for developing into transparencies, and $0.77 for developing into prints for dot grid analysis for a total of $1.04. The sample unit under consideration is one 1m^2 microplot where understory vegetation was clipped. Whereas one moosehorn reading was required for each microplot, four microplots fell within each tree plot whose crown cover was photographed. Thus each sample unit cost $0.26. Stocking estimates by the moosehorn and wide angle lens are compared in Table 1. The relative efficiency of the moosehorn system:

$$RE_{moosehorn} = \frac{(C \times CV^2) \text{ lens}}{(C \times CV^2) \text{ moosehorn}}$$

$$= \frac{26C \times 0.51^2}{1C \times 0.58^2}$$

$$= 20.10$$

Although it produces a higher sample variance, the moosehorn is more efficient than the photographic system by more than twenty times. I have ignored capital costs of the equipment, incidentals of mailing films and slides, and risks of losing a film, slides or prints. The relative efficiency of the moosehorn calculated above is therefore a conservative estimate.

Basal area and percent crown cover may be biologically related, but correlation analysis showed the two variables to be statistically independent (r = 0.26). The wide range of basal area under similar levels of stocking or crown cover (Smith, 1974) and vice versa, is indicative of the complex dynamics of stand development. The low correlation between stocking and density is not unexpected because each varies with aspect, slope, elevation, soils and other factors which are unaccounted for here.

In the first 46 microplots sampled, forage was not separated into grass, forbs and shrubs because of limited manpower. However, it was possible later to isolate the vegetation from 126 plots. In developing regressions for total biomass I used the data from all 172 plots, while for regressions describing grass, forbs and shrubs I used data from 126 plots. This means that regression coefficients in models of the three components are not additive to those of total biomass.

Tables 4, 5, 6, 7, 8, 9 summarize the yield data from all plots. Evidently, variation in yield decreases in the order of grass, forbs and shrubs, and with increasing stocking and density. [Note that coefficients of variation are not percentages].

In subsequent statistical analyses variables are defined as follows:

Independent variables:

X_1 : Basal area (m^2/ha)

X_2 : Percent crown cover by moosehorn

X_3 : Percent crown cover by wide angle lens

Dependent variables:

Y_t : Total forage yield

Y_g : Grass yield

Y_f : Forb yield

Y_s : Shrub yield

All yields are dry weight (Kg/ha) as described in methods.

Table 4

Average dry weight forage yields in the study
area. Data are based on 126 microplots, except
for total which are based on 172 micropolots.

| | Yields (Kg/ha) | | | |
	Grass	Forbs	Shrubs	Total
Mean	88.5	47.8	48.6	159.8
Minimum	0.0	0.0	0.0	0.0
Maximum	743.0	599.0	534.5	1175.4
Stand. dev.	139.3	108.6	97.7	216.3
Coef. of Var.	1.57	2.28	2.01	1.35

Table 5. Average Dry weight biomass (kg/ha) of understory vegetation
in tree patches in the study area. Each moosehorn and yield
datum is based on 4 microplots.

	Basal area (m^2/ha)	% Crown Cover moosehorn	lens	Grass	Forbs	Shrubs	Total
Cherry Cr. 1974	0.0	0	0	–	–	–	207.8
	13.8	25	39	–	–	–	112.0
	16.1	63	63	–	–	–	51.6
	18.4	28	69	–	–	–	126.5
	25.3	67	64	–	–	–	0.0
	27.5	68	63	–	–	–	24.7
	29.8	41	55	–	–	–	250.1
Cherry Cr. 1975	0.0	0	0	48.9	126.5	178.9	354.3
	16.1	49	64	–	–	–	84.9
	20.7	40	42	–	–	–	60.6
	23.0	20	36	–	–	–	80.0
	23.0	60	66	–	–	–	50.6
	29.8	70	40	37.6	3.6	12.5	53.7
	41.3	40	51	–	–	–	125.5
Indian Gardens	0.0	0	0	260.6	32.3	252.5	545.4
	16.1	53	57	306.8	19.6	30.6	357.0
	23.0	70	62	6.1	0.0	31.4	37.5
	29.8	70	53	80.8	4.5	0.0	85.3
	46.0	70	50	0.0	0.0	0.0	0.0

Table 5 continued....

	Basal area (m²/ha)	% Crown Cover moosehorn	lens	Grass	Forbs	Shrubs	Total
Dairy Cr.	0.0	0	0	417.3	344.3	142.7	904.3
	18.4	68	74	12.6	0.0	0.0	12.6
	23.4	75	75	303.5	8.1	9.7	321.3
	25.3	61	45	90.5	21.8	0.0	112.3
	27.5	44	50	10.0	0.0	0.0	10.0
	34.4	69	68	6.8	0.0	0.0	6.8
	36.7	70	60	38.7	0.0	0.0	38.7
Mountain View	0.0	0	0	102.2	262.1	120.5	484.8
	13.8	61	62	53.9	57.4	9.0	120.3
	23.0	60	71	3.9	83.0	28.1	115.0
	23.0	61	49	28.8	1.5	0.0	30.3
	23.0	88	78	15.7	0.8	19.8	36.3
	39.8	91	90	2.3	0.5	8.1	10.9
	41.3	45	55	44.5	8.6	0.0	53.1
Dead '74	20.4	39	40	66.0	278.5	129.9	474.4
	25.3	72	72	14.9	0.0	0.0	14.9
Heffley Cr. - Road	0.0	0	0	62.7	86.9	272.4	422.0
	13.8	76	75	19.0	13.7	60.5	93.2
	16.1	83	67	4.7	0.0	0.0	4.7
Hill	0.0	0	0	554.4	61.6	132.2	748.2
	20.7	52	57	104.9	10.5	0.0	115.4
	20.7	64	58	48.2	10.7	68.0	126.9
	20.7	71	75	77.8	0.0	2.0	79.8

Table 6. Grass yields (kg/ha) under various stand stocking and density.
Crown cover data are from moosehorn % CC class 1: 0-10;
2: 11-30; 3: 31-70; 4: 71-96.

Basal area (m²/ha)	0.0 - 11.5				11.6 - 23.0				23.1 - 34.4				34.5 - 46.0			
Crown cover class	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
	30.7				13.6	6.3	6.4		0.5	21.9	35.7		25.8	0.0	0.0	
	76.6					526.4	11.5			23.3	83.5			0.0	0.0	
	2.7					234.5	0.0			80.5	9.3			63.4	13.5	
	88.6					217.6	380.4			119.1	181.7			57.9	20.4	
	67.7					248.5	388.5			124.1	37.7			0.0	0.0	
	36.5					169.1	0.0			76.7	0.0			0.0	0.0	
	193.6					276.0	72.1			42.0	0.0			0.0	0.0	
	364.6					0.0	42.9			28.5	6.6			0.0	9.0	
	263.0					5.7	44.8			0.0	43.1			0.0		
	221.1					0.0	14.1			11.1				44.1		
	360.3					45.1	15.7			16.4				108.2		
	412.4					0.0	22.1			10.6						
	272.6					0.0	11.0			10.0						
	623.7					15.5	4.0			0.0						
	124.0					0.0	57.9									
	180.0					0.0	0.0									

Basal area (m²/ha)	0.0 - 11.5				11.6 - 23.0				23.1 - 34.4				34.5 - 46.0			
Crown cover class	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
	53.2						136.0	18.7								
	51.5						34.9	0.0								
	75.9						0.0	0.0								
	25.0						112.6	29.2								
	48.9						85.4	91.0								
	101.0						52.2	8.1								
	621.4						8.2									
	743.0						5.7									
	206.9						197.0									
	396.0						6.0									
							41.4									
							175.0									
							85.5									
							77.0									
							1.0									
							128.7									
							83.0									
Mean	215.92						90.13	55.35			40.30	44.18			24.87	5.36
St.dev.	205.59						116.00	109.4			42.44	58.21			37.71	8.01
Coef Var.	0.95						1.29	1.98			1.05	1.32			1.08	1.49

Table 7. Forb yields (kg/ha) under various stand stocking and density.
Crown cover data are from moosehorn. % CC class 1: 0-10;
2: 11-30; 3: 31-70; 4: 71-96.

Basal area (m²/ha)	0.0 - 11.5				11.6 - 23.0				23.1 - 34.4				34.5 - 46.00			
Crown cover class	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
	254.8					499.7	0.0	0.0		0.0	0.9	0.0		34.0	0.0	0.0
	18.5						0.0	0.0			0.0	0.0			0.0	0.0
	197.8						0.0	0.0			0.0	13.6			0.0	0.0
	178.7						78.4	0.0			12.6	0.0			0.0	0.0
	110.5						0.0	32.4			0.0	17.3			0.0	0.0
	18.7						0.0	21.7			54.4	0.0			0.0	1.8
	0.0						0.0	0.0			20.3	0.0			0.0	0.0
	52.4						0.0	0.0			0.0	0.0			0.0	0.0
	40.5						0.0	16.9			0.0	0.0			0.0	
	36.2						0.0	0.0			0.0				0.0	
	578.6						0.0	0.0			0.0				0.2	
	74.4						124.6	2.3			0.0					
	599.0						146.0	1.0			0.0					
	125.3						39.5	2.2			0.0					
	304.3						5.8	33.4								
	421.7						0.0	0.0								
	267.9						15.3	0.0								
	54.5						56.0	0.0								
	225.0						141.2	0.0								

Table 7 continued ....

Basal area (m²/ha)	0.0 - 11.5				11.6 - 23.0				23.1 - 34.4				34.5 - 46.00			
Crown cover class	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
	25.2						130.2	0.0								
	37.5						300.7	0.0								
	60.0						183.2	0.0								
	61.1						18.9									
	76.0						0.2									
	1.1						0.0									
	108.1						0.0									
							41.7									
							0.4									
							0.0									
							0.0									
							42.1									
							0.0									
							0.0									
Mean	151.07						40.13	5.00			6.30	3.43			0.02	0.23
St.dev.	167.17						70.61	10.66			15.13	6.88			0.06	0.64
Coef.Var.	1.11						1.76	2.13			2.40	2.01			3.00	2.78

Table 8. Shrub yields (kg/ha) under various stand stocking and density. Crown cover data are from moosehorn. %CC class 1: 0-10; 2: 11-30; 3: 31-70; 4: 71-95.

Basal area (m²/ha)	0.0 – 11.5				11.6 – 23.0				23.1 – 34.4				34.5 – 46.0			
Crown cover class	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
	0.0					0.0	0.0	0.0		0.0	0.0	0.0		0.0	0.0	0.0
	131.8						122.5	125.7			0.0	27.5			0.0	0.0
	147.5						0.0	0.0			0.0	22.4			0.0	0.0
	178.5						0.0	6.3			0.0	0.0			0.0	0.0
	58.5						0.0	0.0			0.0	0.0			0.0	0.0
	331.4						32.3	18.6			0.0	0.0			0.0	34.3
	0.0						0.0	0.0			0.0	0.0			0.0	0.0
	192.4						0.0	0.0			0.0	0.0			0.0	9.0
	534.5						0.0	36.1			0.0	0.0		0.0		
	283.2						0.0	20.8		0.0				0.0		
	236.5						0.0	27.2		0.0				0.0		
	117.3						0.0	13.0		0.0						
	0.0						9.4	18.0		0.0						
	217.1						34.4	121.8		0.0						
	35.9						0.0	0.0								
	0.0						0.0	0.0								
	165.4						0.0	0.0								
	280.5						0.0	0.0								

Table 8 continued ...

Basal area (m²/ha)	0.0 - 11.5				11.6 - 23.0				23.1 - 34.4				34.5 - 46.0			
Crown cover class	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
	141.0						0.0	0.0								
	393.8						306.1	12.9								
	321.0						153.2	0.0								
	233.9						60.1	0.0								
	34.9						18.2									
	136.9						102.1									
	249.0						0.0									
	108.1						0.0									
							0.0									
							0.0									
							0.0									
							259.1									
							0.0									
							0.0									
							7.9									
Mean	174.20						33.49	18.20			0.0	5.54			0.0	5.41
St. Dev.	133.97						74.80	33.77			undefined	11.08			undefined	12.09
Coef Var.	0.77						2.23	1.97			"	2.00			"	2.24

Table 9. Total forage yields (kg/ha) under various stand stocking and density. Crown cover data are from moosehorn. %CC class 1: 0 - 10; 2: 11-30; 3: 31-70; 4: 71-95.

Basal area (m²/ha) 0.0 - 11.5				11.6 - 23.0				23.1 - 34.4				34.5 - 46.0			
1	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
186.5				111.3	163.5	124.6	57.6		0.5	235.0	34.3		124.5	182.5	0.0
132.6				59.2	132.4	147.0	111.4			298.5	20.5		59.8	89.5	0.0
285.5				181.5	85.4	38.6	6.4			147.4	23.6			105.5	0.0
226.7					126.2	59.5	137.2			323.2	0.0			0.0	13.5
348.0					69.7	50.5	0.0			20.5	0.0			63.4	20.4
445.8					99.4	33.4	386.7			0.0	0.0			57.9	0.0
326.7					59.3	98.9	420.9			22.8	35.7			0.0	34.3
386.6					20.0	11.6	40.3			23.3	111.0			0.0	0.0
193.6					513.2	66.9	72.1			80.5	45.3			0.0	9.0
609.4						60.7	42.9			131.7	181.7			0.0	
838.4						100.6	97.8			124.1	55.0			0.0	
540.5						80.0	34.9			131.1	0.0			44.1	
1175.4						86.5	42.9			62.3	0.0		108.4		
604.1						32.5	37.4			28.5	6.6				
871.6						3.4	30.0			0.0	43.1				
966.1						6.3	128.0			11.1					
464.2						648.9	91.3			16.4					
601.7						234.5	0.0			10.6					

Table 9 continued ...

Basal area (m²/ha)	0.0 - 11.5				11.6 - 23.0				23.1 - 34.4				34.5 - 48.0			
Crown cover class	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
	486.5						296.0	18.7			10.0					
	386.5						248.5	0.0			0.0					
	441.9						201.4	0.0								
	444.0						276.0	42.1								
	407.0						0.0	91.0								
	394.9						5.7	8.1								
	717.4						0.0									
	955.9						45.1									
	457.0						124.6									
	612.2						155.4									
							89.4									
							5.8									
							0.0									
							151.3									
							90.9									
							141.2									
							336.1									
							43.9									
							128.7									

Table 9 continued ....

Basal area (m^2/ha)	0.0 - 11.5				11.6 - 23.0				23.1 - 34.4				34.5 - 48.0			
Crown cover class	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
							90.9									
							548.9									
							539.3									
							295.5									
							45.3									
							108.0									
							197.7									
							6.0									
							83.1									
							175.4									
							85.5									
Mean	518.08				117.33	141.02	133.33	79.07			83.85	37.12		92.15	50.10	8.58
St. Dev.	256.63				61.37	146.04	145.55	108.35			100.81	50.05		44.15	58.37	12.22
Coef Var.	0.50				0.52	1.04	1.09	1.37			1.20	1.35		0.50	1.17	1.42

Scattergrams (Figures 10 to 24 inclusive) indicated non-linear relationships between the dependent and independent variables. Therefore, strict linear models were not examined for regression modeling. Constants in X + 1 and Y + 1 in hyperbolic and logarithmic analyses respectively are used to avoid mathematical problems because in some cases X and Y equaled zero. The logarithmic transformation makes variances along the regression line more uniform. For the logarithmic model, the standard errors of the estimate were transformed into nonlogarithmic form. The transformation procedure is as follows:

$$\text{The SEE} = \sqrt{SS_r/df_r}$$

where SS_r = sum of squares residual

df_r = degrees of freedom residual

Transformation:

$$SS_r = \sum_{j=1}^{n} \left[(y_j + 1) - 10^{(b_o + \sum_i b_i X_{ij})} \right]^2$$

$j = j^{th}$ forage yield

n = number of observations

$Y_j = Y_{tj}, g_j, f_j, s_j$ individually

$X_i = i^{th}$ independent variable; i = 1, 2 here

b_o, b_i = regression coefficients defined formally.

$$df_r = n-m-1$$

m = number of independent variables in the significant

model under consideration.

$$SEE = \sqrt{SS_r/df_r}$$

$$= \sum_{j=1}^{n} \left[(y_j + 1) - 10^{(b_o + \sum_i b_i X_{ij})} \right] \bigg/ [n-m-1]^{1/2}$$

The models reported below (Tables 10, 11) were significant

at 95 percent probability level. Analyses were by least squares

technique - elimination procedure. Some dependent variables are

described by two significant models; the models are in the order they

were encountered through elimination. The second model is shown for

checking how much precision is lost by dropping one significant variable.

This becomes relevant when it may be costly to measure a variable.

Coefficients of determination are not transformed to nonlogarithmic form:

therefore it would be unwise to compare fitness of hyperbolic with

logarithmic models using R^2 values. It is acceptable to compare

between logarithmic models using these values.

Better fit of logarithmic models is evident. Yields are also

shown graphically in figures 10 -- 24 inclusive.

Enlarging plot size by combining data from 4 microplots

(Table 5) did not reduce standard errors significantly. This resulted

in an increase of standard errors in some logarithmic models. Apparently,

Table 10. Hyperbolic models significant at 95 percent
probability level: forage yields.

$Y = b_o + b_1 X_1 + b_2 (1/X_1 + 1)$	SEE	%R^2	F
$Y_t = 141.356 - 2.9378 X_1 + 365.387 \ (1/X_1 + 1)$	147.212	54.238	100.150
$: 71.7137 + 444.595 \ (1/X_1 + 1)$	148.468	53.178	193.097
$Y_g = 47.9099 + 170.009 \ (1/X_1 + 1)$	123.035	22.633	36.275
$Y_f = 15.1861 + 136.377 \ (1/X_1 + 1)$	95.1174	23.952	39.056
$Y_s = 9.0021 + 165.614 \ (1/X_1 + 1)$	73.6212	43.673	96.143

$Y = b_o + b_1 X_2 + b_2 \ (1/X_2 + 1)$			
$Y_t = 169.248 - 1.4151 X_2 + 345.092 \ (1/X_2 + 1)$	146.974	54.386	100.748
$: 81.902 + 164.971 \ (1/X_2 + 1)$	148.661	53.060	192.135
$Y_g = 52.4075 + 164.584 \ (1/X_2 + 1)$	123.304	22.295	35.578
$Y_f = 144.7689 - 1.8557 X_2$	92.9141	27.430	46.881
$Y_s = 13.2240 + 161.056 \ (1/X_2 + 1)$	73.7918	43.410	95.126

$Y = b_o + b_1 X_1 + b_2 \ (1/X_1 + 1) + b_3 X_2 + b_4 \ (1/X_2 + 1)$			
$Y_t = 167.764 + 348.384 \ (1/X_1 + 1) - 1.5260 X_2$	146.269	54.820	102.538
$: 71.7132 + 444.595 \ (1/X_1 + 1)$	148.468	53.178	193.079
$Y_g = 47.9099 + 170.009 \ (1/X_1 + 1)$	123.035	22.633	36.275
$Y_f = 259.417 - 5.9193 X_1 - 3363.590 \ (1/X_1 + 1)$ $+3255.490 \ (1/X_2 + 1)$	92.359	29.454	16.979
$: 18.5076 + 133.330 \ (1/X_2 + 1)$	95.048	24.060	39.295
$Y_s = 9.0091 + 165.614 \ (1/X_1 + 1)$	73.621	43.673	96.143

Table 10 continued...

$Y = b_o + b_1 X_3 + b_2 (1/X_3 + 1)$	SEE	$\%R^2$	F
$Y_t = 200.798 - 1.8972 X_3 + 314.084 \ (1/X_3 + 1)$	147.617	53.986	99.138
$Y_g = 52.3948 + 164.643 \ (1/X_3 + 1)$	123.293	22.308	35.605
$Y_f = 144.550 - 1.9323 X_3$	94.103	25.567	42.529
$Y_s = 13.216 + 161.093 \ (1/X_3 + 1)$	73.783	43.426	95.181

$Y = b_o + b_1 X_1 + b_2 (1/X_1 + 1) + b_3 X_3 + b_4 (1/X_3 + 1)$	SEE	$\%R^2$	F
$Y_t = 304.978 - 3.6461 X_1 - 2.0709 X_3$			
$+209.885 \ (1/X_3 + 1)$	145.208	55.739	70.521
$: 170.698 - 3.4118 X_1 + 344.718 \ (1/X_3 + 1)$	146.959	54.395	100.788
$Y_g = 213.932 - 3.1847 X_1 - 1.1880 X_3$	121.524	25.131	20.643
$: 190.743 - 4.9396 X_1$	123.509	22.037	35.047
$Y_f = 144.550 - 1.9323 X_3$	94.103	25.567	42.592
$Y_s = 9.0021 + 165.614 \ (1/X_1 + 1)$	73.621	43.673	96.145

Table 11. Logarithmic$_{10}$ models significant at 95 percent
probability level: forage yields.

$\log(Y+1) = b_o + b_1 X_1$	SEE	$\%R^2$	F
$\log(Y_t+1) = 2.5699 - 0.0423X_1$	130.590	34.410	89.189
$\log(Y_g+1) = 2.0582 - 0.0349X_1$	44.104	27.171	46.262
$\log(Y_f+1) = 1.6524 - 0.0443X_1$	116.505	39.514	81.007
$\log(Y_s+1) = 1.6258 - 0.0452X_1$	13.373	38.477	77.550

$\log(Y+1) = b_o + b_1 X_2$	SEE	$\%R^2$	F
$\log(Y_t+1) = 2.5206 - 0.0167X_2$	124.434	29.930	72.610
$\log(Y_g+1) = 2.0173 - 0.0130X_2$	41.084	20.364	31.709
$\log(Y_f+1) = 1.7835 - 0.0201X_2$	22.399	43.455	95.293
$\log(Y_s+1) = 1.5435 - 0.0163X_2$	10.810	26.955	43.745

$\log(Y+1) = b_o + b_1 X_1 + b_2 X_2$	SEE	$\%R^2$	F
$\log(Y_t+1) = 2.7357 - 0.0289X_1 - 0.0089X_2$	200.815	39.428	55.003
: $2.5699 - 0.0423X_1$	145.987	34.410	89.189
$\log(Y_g+1) = 2.0582 - 0.0349X_1$	44.108	27.171	46.262
$\log(Y_f+1) = 1.8897 - 0.0228X_1 - 0.0131X_2$	29.945	48.619	58.195
: $1.7835 - 0.0208X_2$	22.398	43.455	95.293
$\log(Y_s+1) = 1.6258 - 0.0452X_1$	13.375	38.477	77.550

Table 11 continued...

$\log(Y+1) = b_o + b_1 X3$	SEE	$\%R^2$	F
$\log(Y_t+1) = 2.6169 - 0.0185X_3$	150.326	28.968	69.328
$\log(Y_g+1) = 2.1062 - 0.0154X_3$	50.601	24.320	39.842
$\log(Y_f+1) = 1.7829 - 0.0209X_3$	22.409	40.560	86.614
$\log(Y_s+1) = 1.6382 - 0.0189X_3$	13.662	31.089	55.941

$\log(Y+1) = b_o + b_1 X_1 + b_2 X_3$	SEE	$\%R^2$	F
$\log(Y_t+1) = 2.7749 - 0.0296X_1 - 0.0093X_3$	221.696	38.655	53.245
$: 2.5699 - 0.0423X_1$	130.590	34.407	89.174
$\log(Y_g+1) = 2.2138 - 0.0232X_1 - 0.0080X_3$	66.179	30.605	27.124
$: 2.0582 - 0.0350X_1$	44.104	27.171	46.262
$\log(Y_f+1) = 1.9013 - 0.0255X_1 - 0.0128X_3$	30.869	47.446	55.522
$: 1.7829 - 0.0209X_3$	22.409	40.560	84.614
$\log(Y_s+1) = 1.7902 - 0.0327X_1 - 0.0084X_3$	21.353	41.725	44.034
$: 1.6258 - 0.0452X_1$	13.373	38.477	55.473

FIG.10. RELATIONSHIP BETWEEN GRASS YIELDS AND STAND DENSITY

$Y=(114.341 \times 0.923^X)-1.$
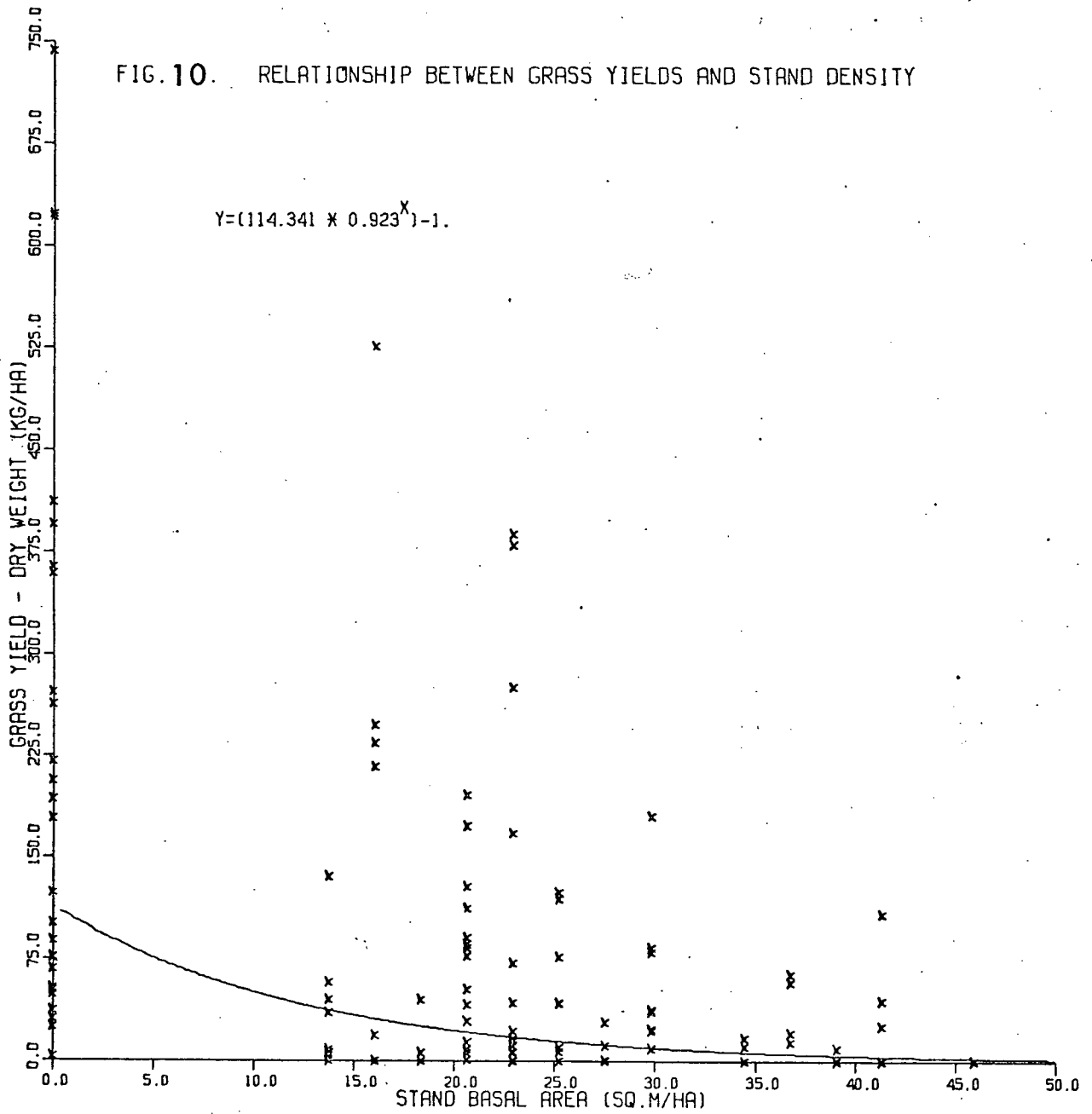
FIG.11. RELATIONSHIP BETWEEN FORB YIELDS AND STAND DENSITY

$Y = (49.916 * 0.903^X) - 1.$
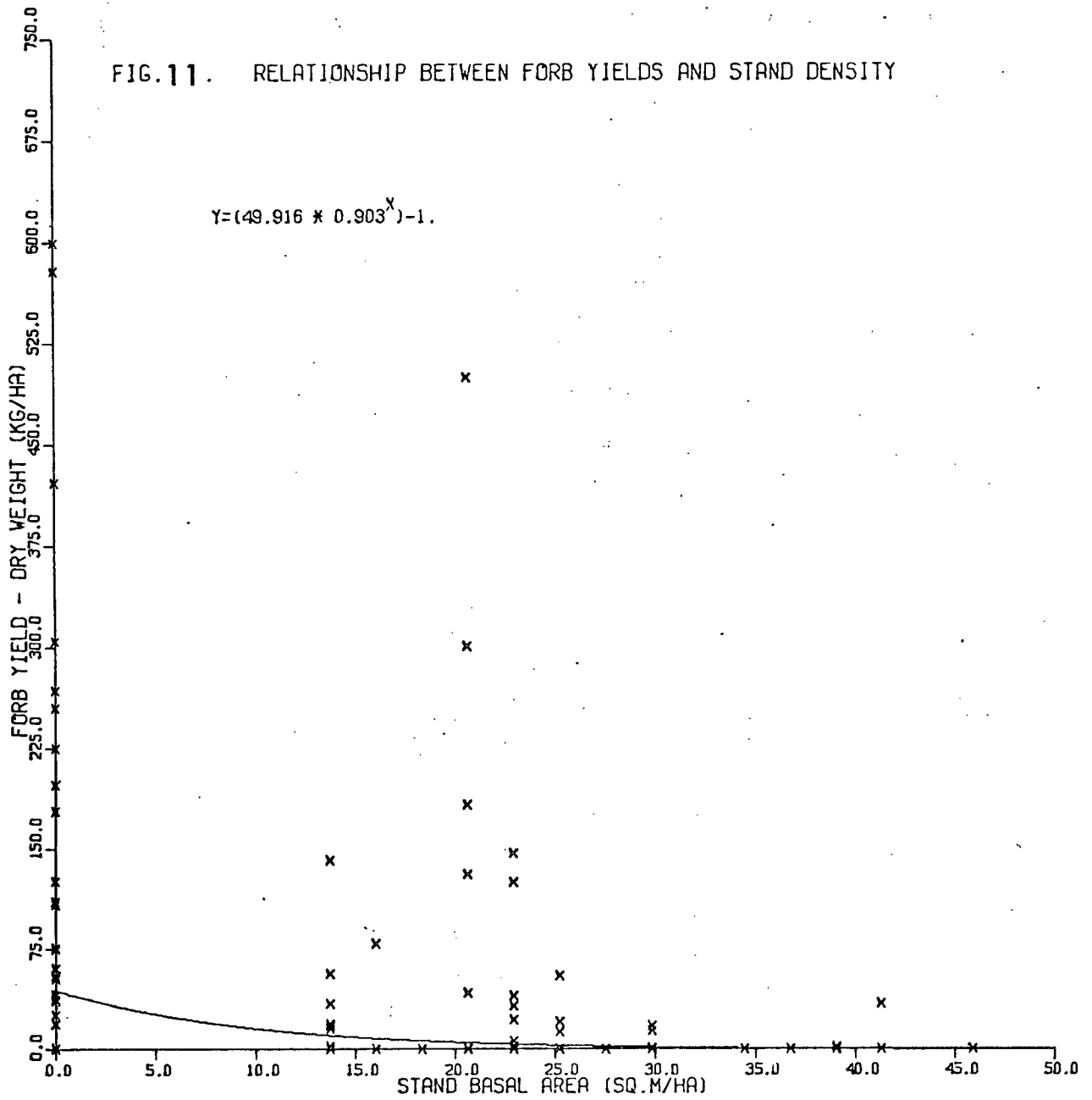
FIG.12. RELATIONSHIP BETWEEN SHRUB YIELDS AND STAND DENSITY

$Y=(42.247 * 0.901^X)-1.$

FIG.1 3.   RELATIONSHIP BETWEEN GRASS YIELDS AND STOCKING

$Y=(104.064 * 0.971^X)-1.$

FIG.14. RELATIONSHIP BETWEEN FORB YIELDS AND STOCKING

$Y=(60.744 \times 0.955^{X})-1.$
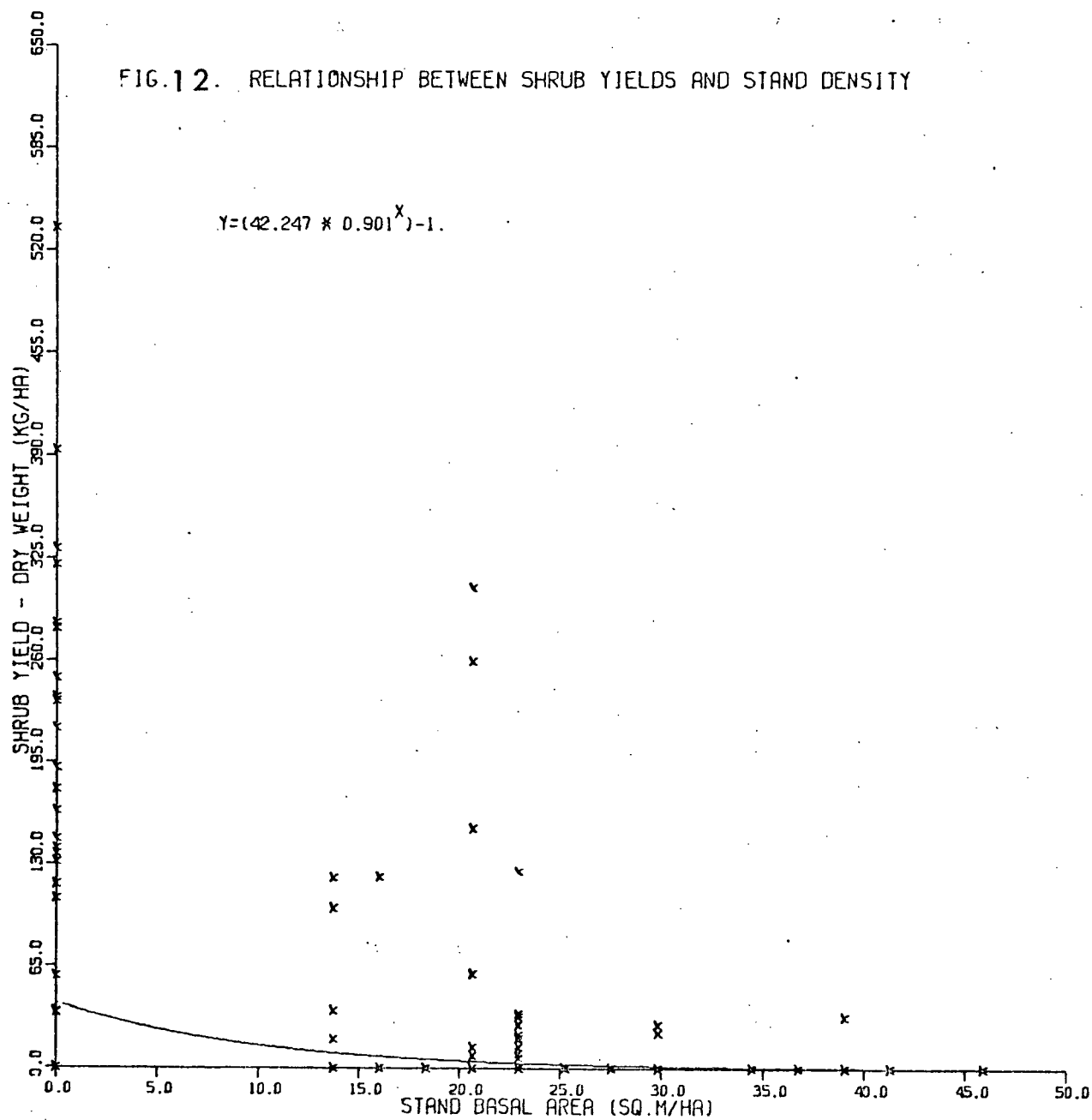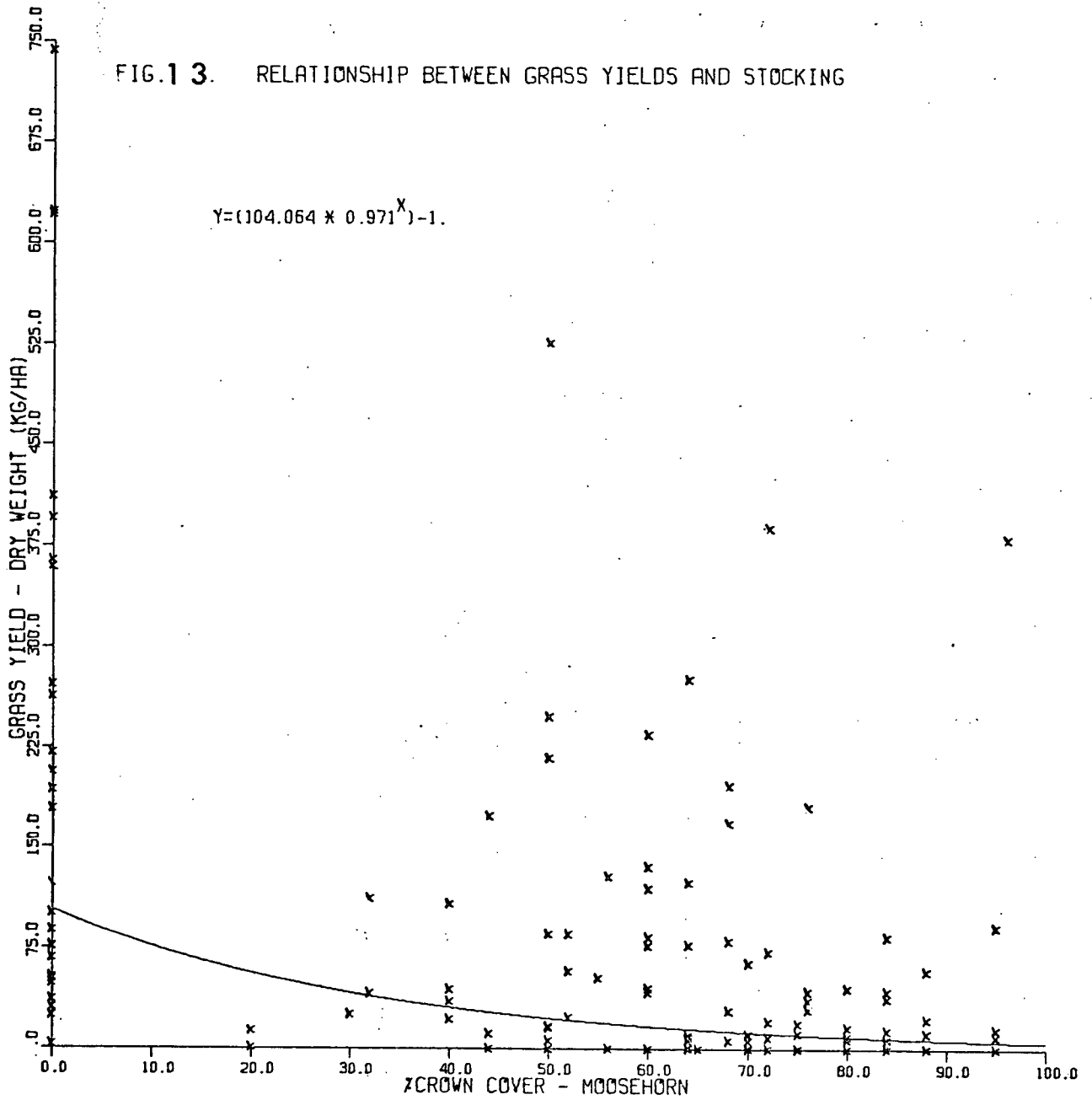
FIG.15. RELATIONSHIP BETWEEN SHRUB YIELDS AND STOCKING

$Y=(34.954 * 0.963^X)-1.$
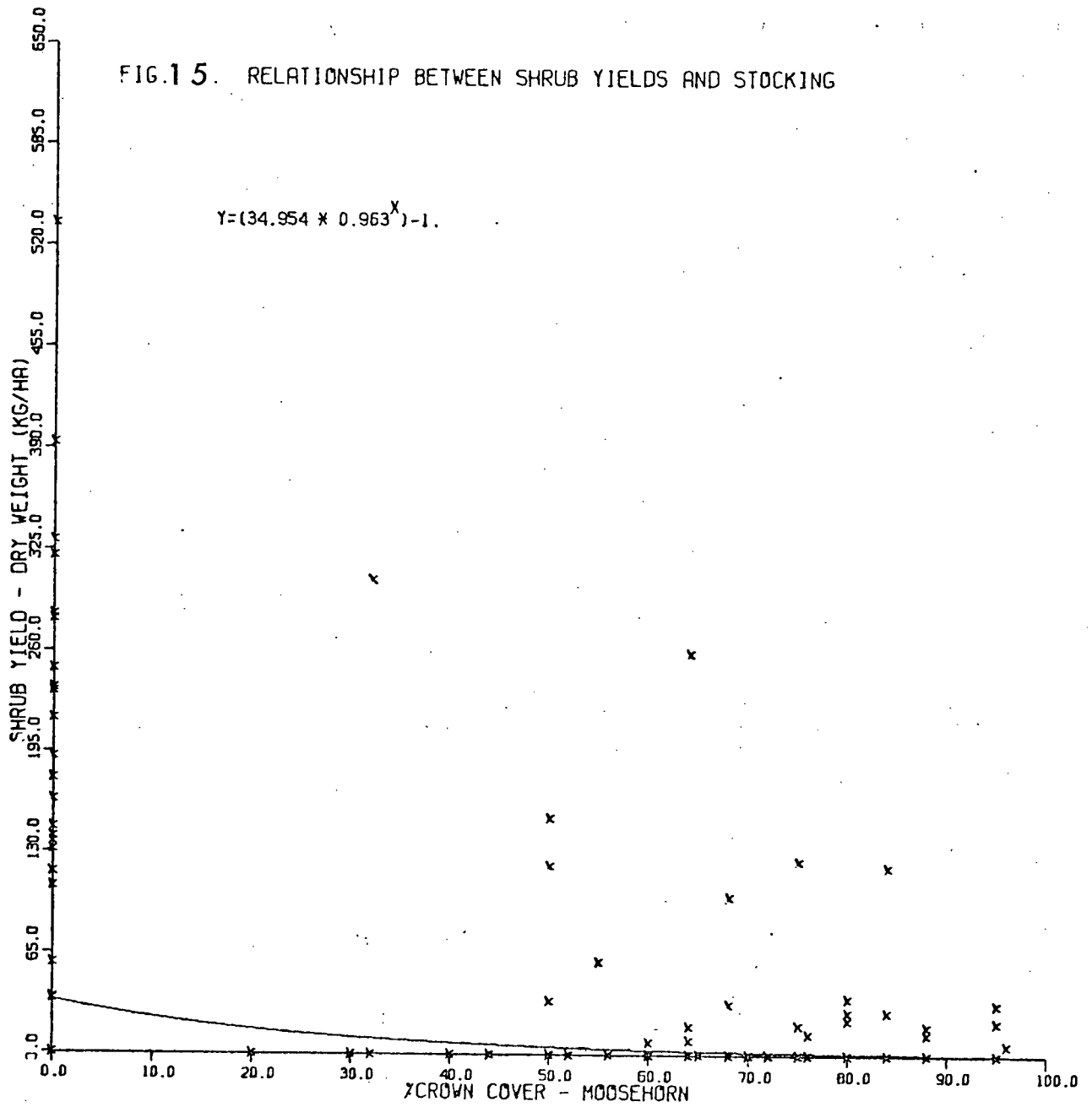
FIG. **16**. RELATIONSHIP BETWEEN GRASS YIELDS AND STOCKING

$Y = (127.703 \times 0.965^X) - 1.$
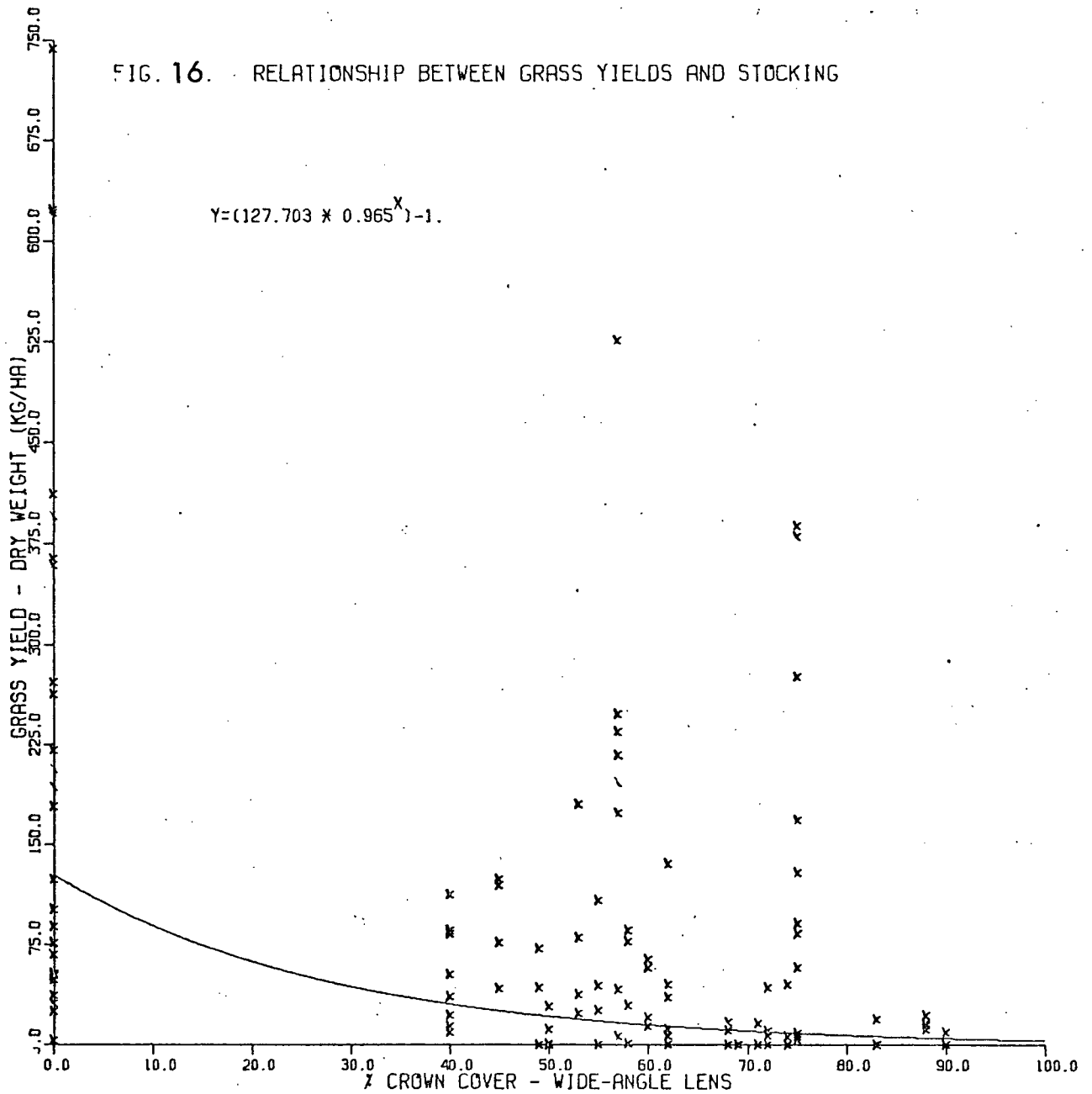
FIG. **17.**   RELATIONSHIP BETWEEN FORB YIELDS AND STOCKING

$Y=(60.660 \times 0.953^X)-1.$
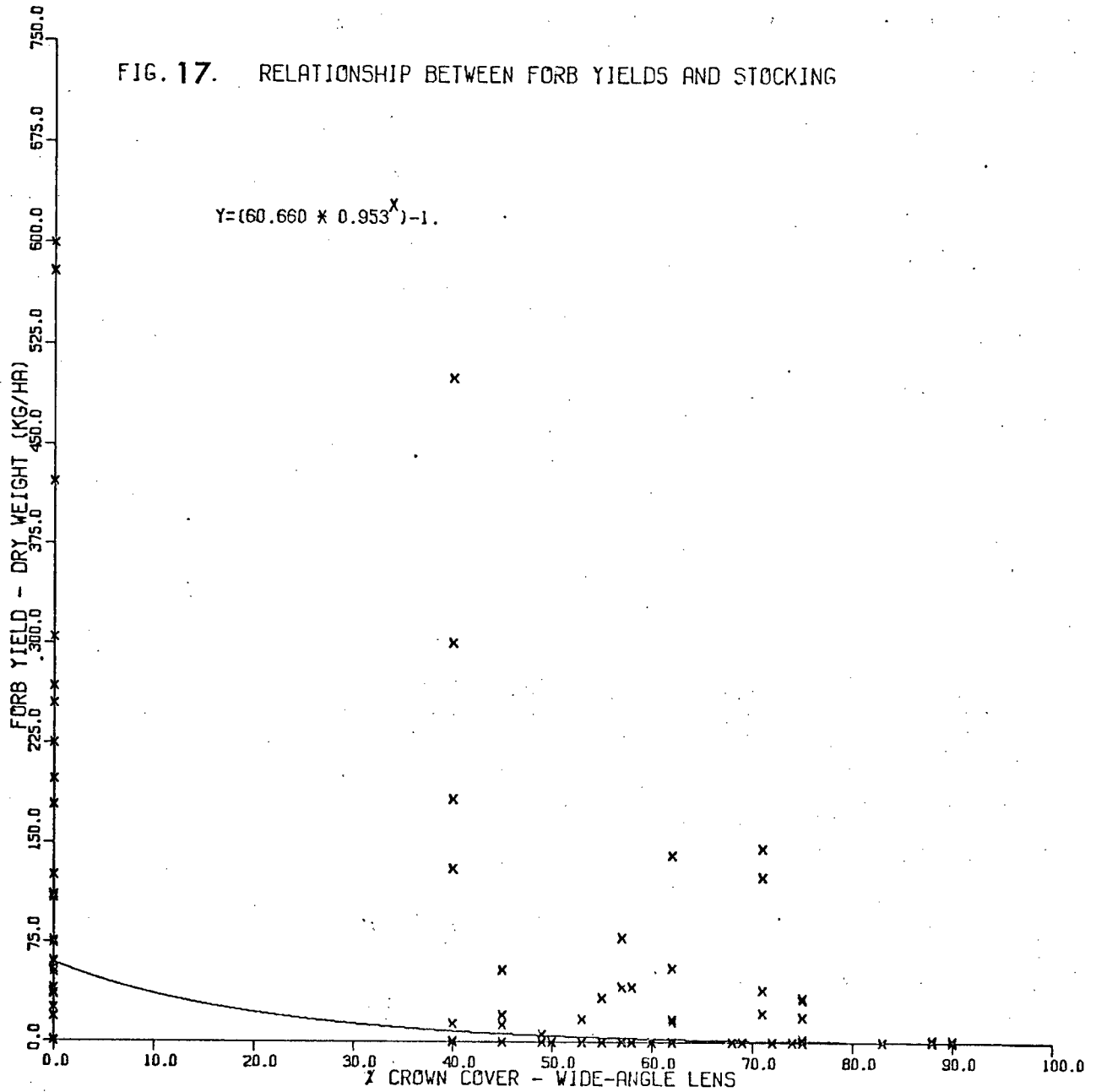
FIG. **18.** RELATIONSHIP BETWEEN SHRUB YIELDS AND STOCKING

$Y = (43.471 \times 0.957^X) - 1.$
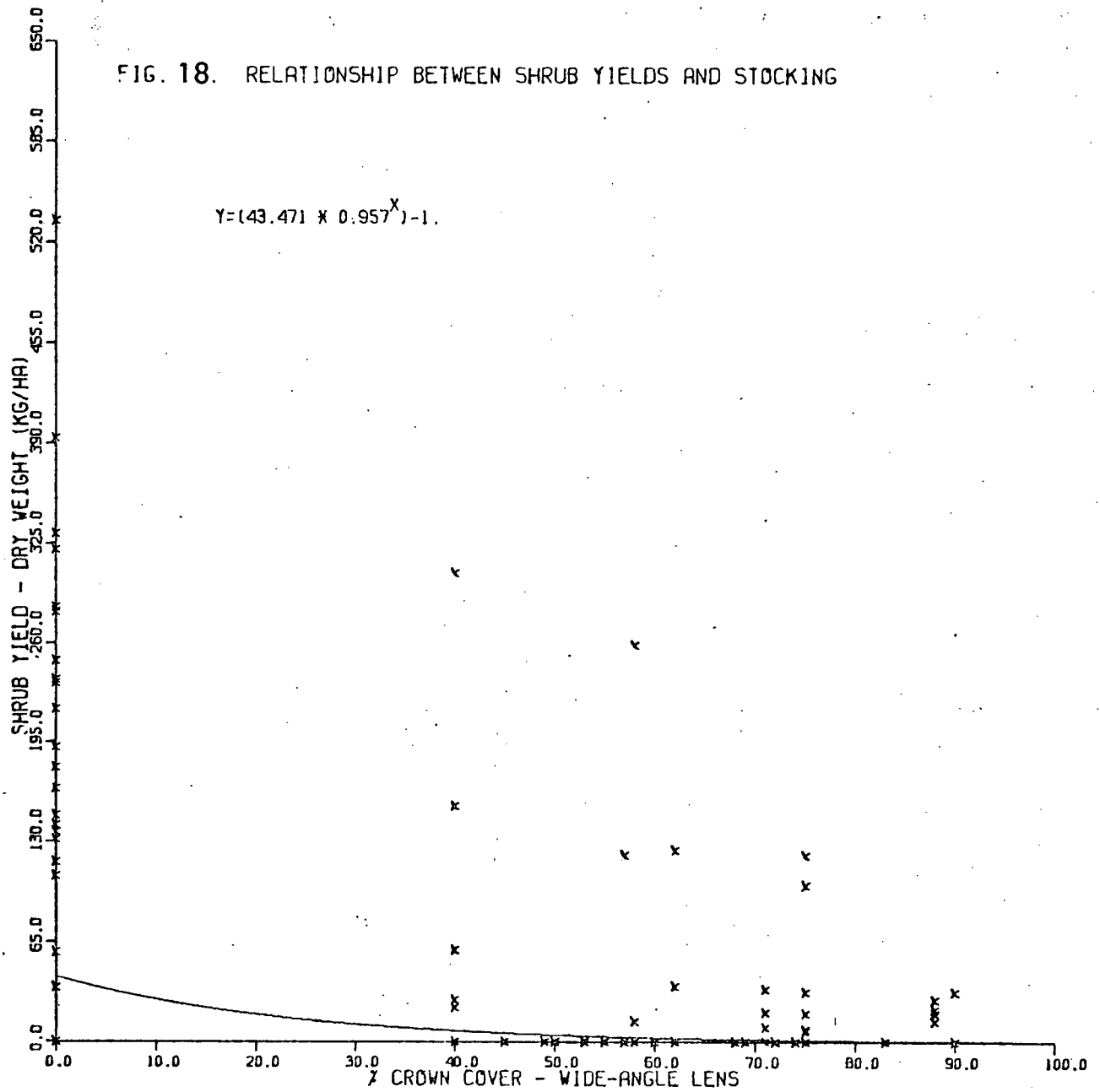
FIG. 19. RELATIONSHIP BETWEEN DRY WT. BIOMASS AND STAND DENSITY

GR: $Y = (114.341 \times 0.923^X) - 1.$

FO: $Y = (49.916 \times 0.903^X) - 1.$

SH: $Y = (42.247 \times 0.901^X) - 1.$

FIG. 20. RELATIONSHIP BETWEEN DRY WT. BIOMASS AND STOCKING

GR: $Y = (104.064 * 0.971^X) - 1.$

FO: $Y = (60.744 * 0.955^X) - 1.$

SH: $Y = (34.954 * 0.963^X) - 1.$

GRASS

FORBS

SHRUBS

BIOMASS – DRY WT. (KG/HA)

%CROWN COVER – MOOSEHORN

FIG. 21. RELATIONSHIP BETWEEN DRY WT. BIOMASS AND STOCKING

GR: $Y=(127.703 \times 0.965^X)-1.$

FO: $Y=(60.660 \times 0.953^X)-1.$

SH: $Y=(43.471 \times 0.957^X)-1.$

GRASS

FORBS

SHRUBS

BIOMASS - DRY WT. (KG/HA)

% CROWN COVER - WIDE-ANGLE LENS
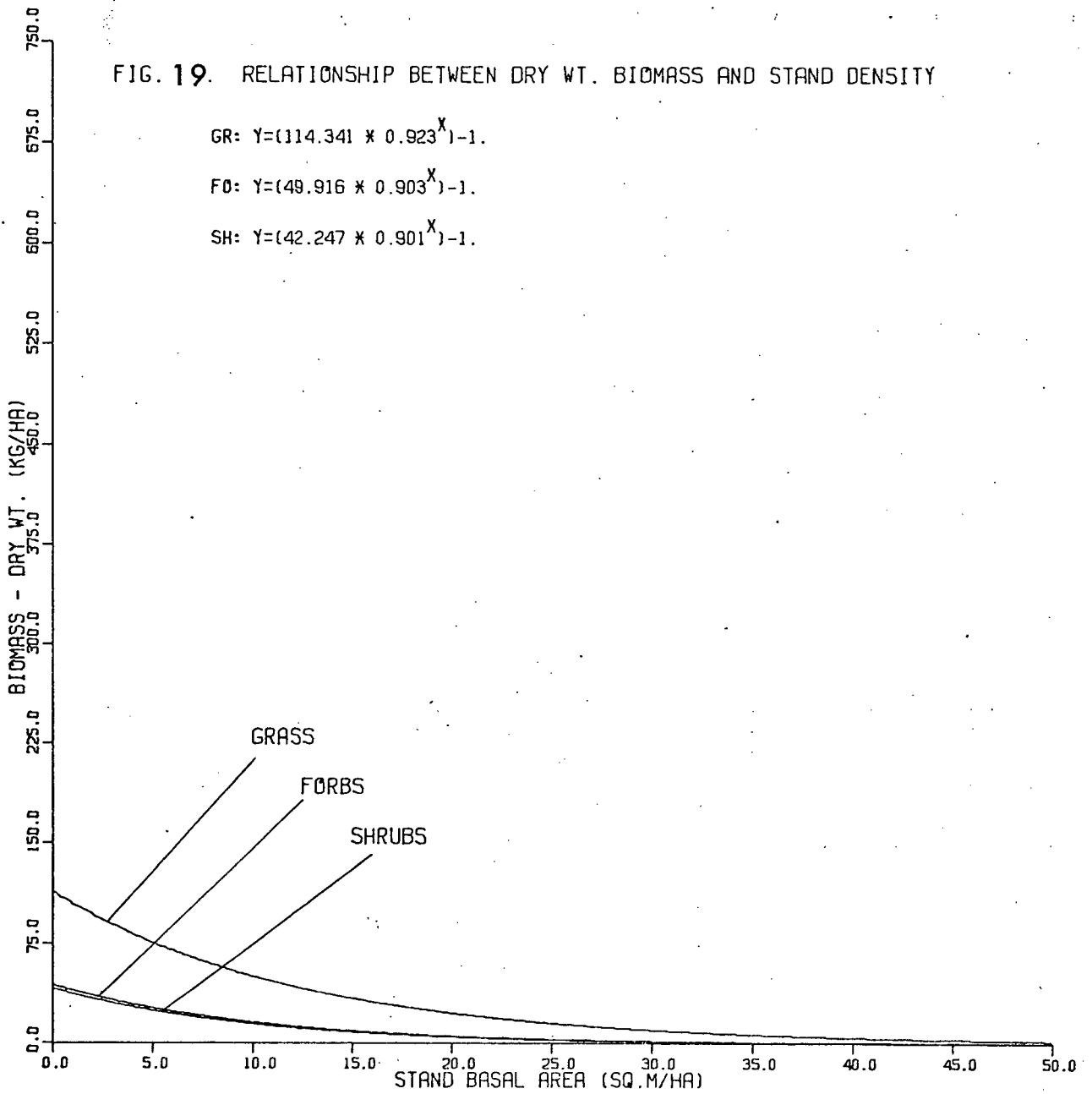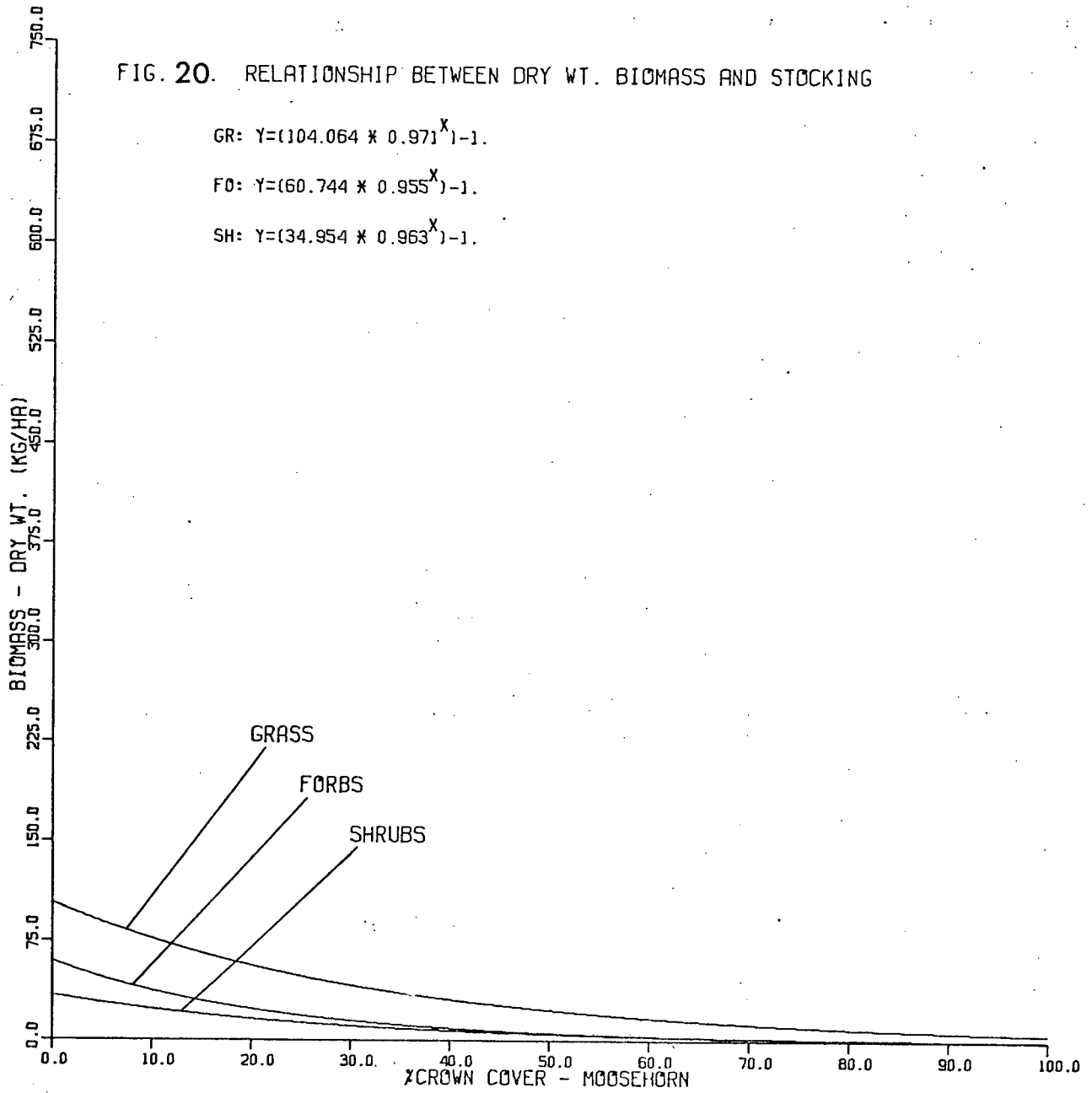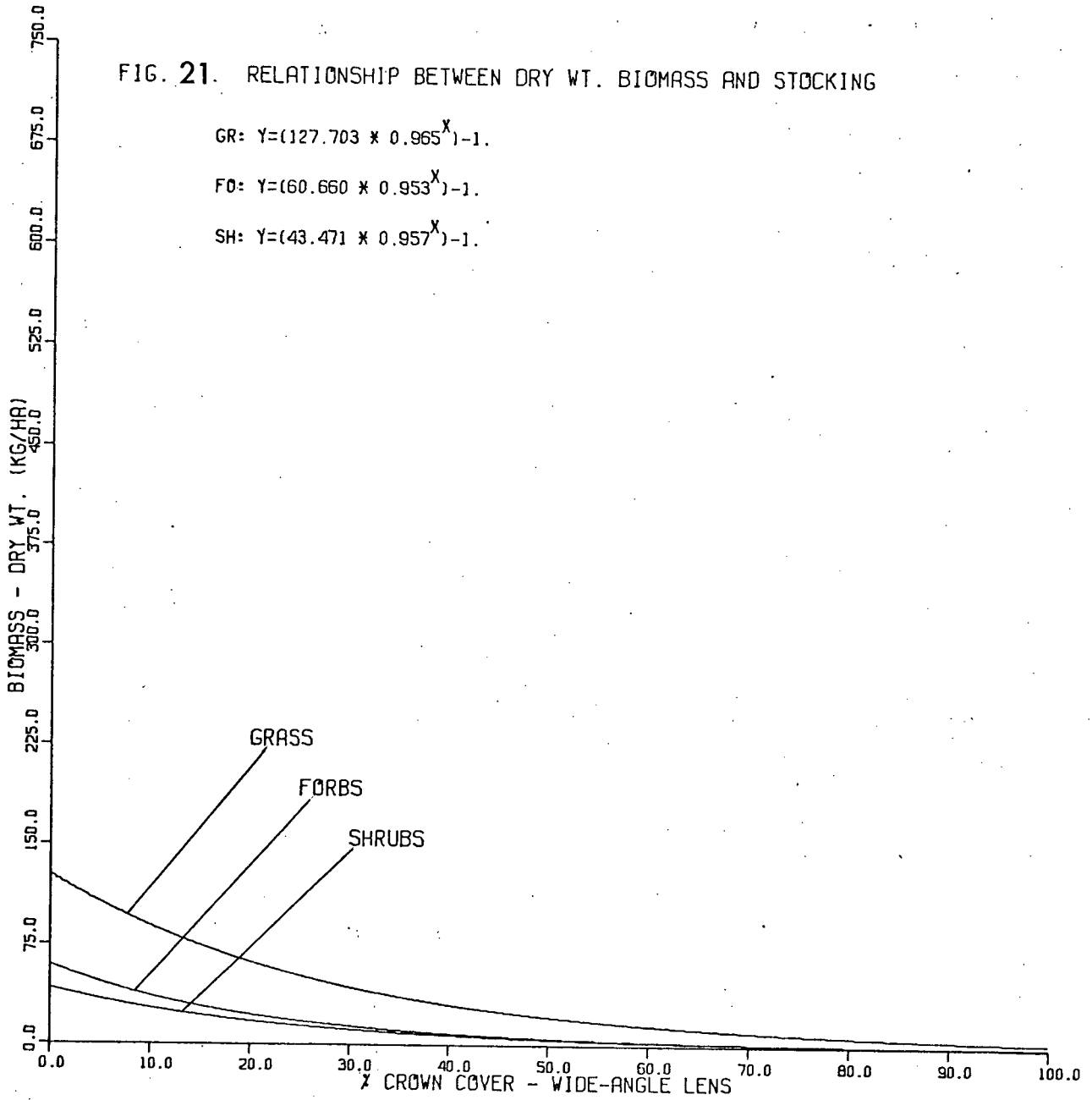
FIG. 22. RELATIONSHIP BETWEEN TOTAL FORAGE YIELDS AND STAND DENSITY

$Y=(371.449 * 0.907^X)-1.$
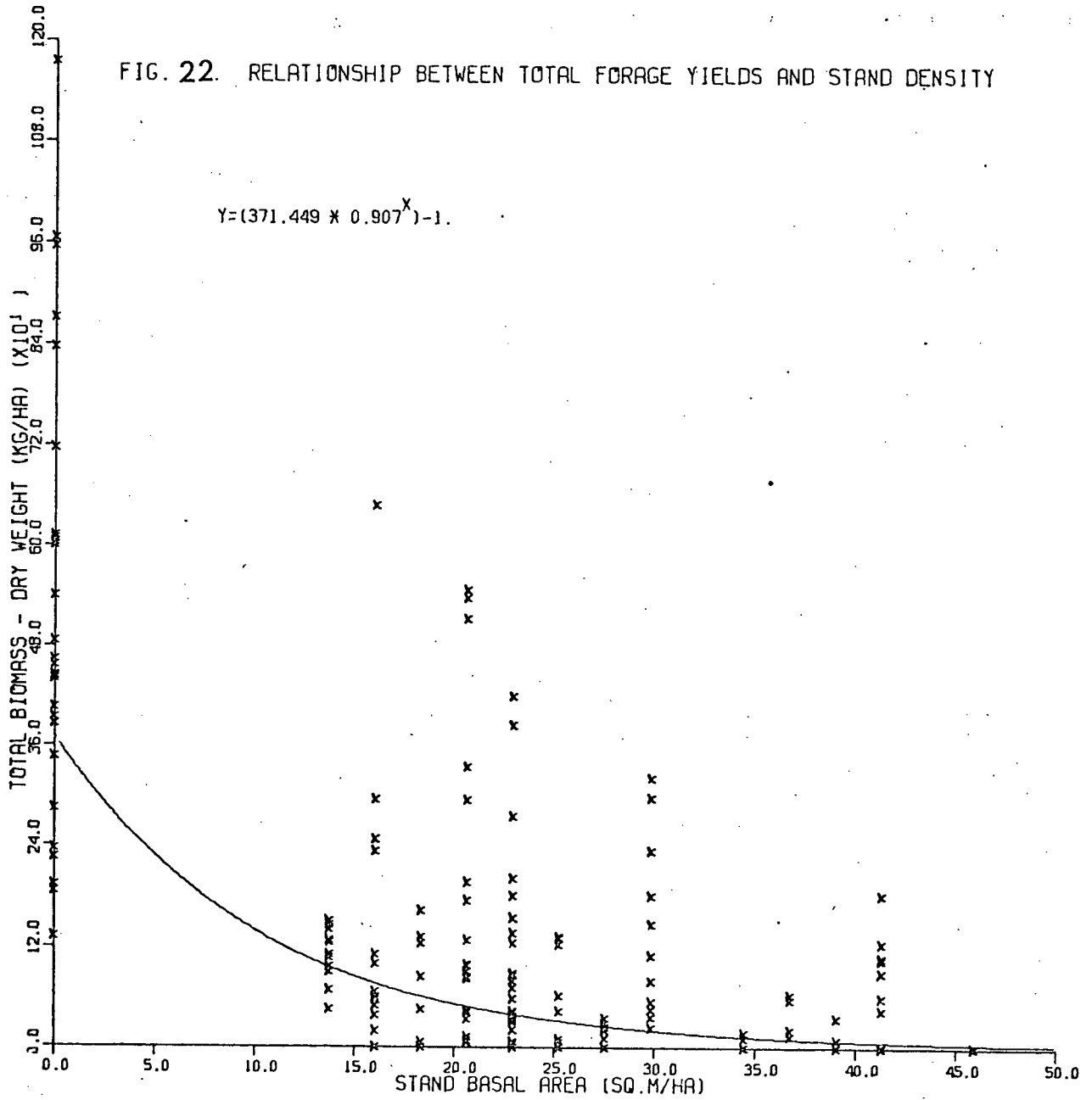
FIG. 23.   RELATIONSHIP BETWEEN TOTAL FORAGE YIELDS AND STOCKING

$Y = (331.589 \times 0.962^X) - 1.$
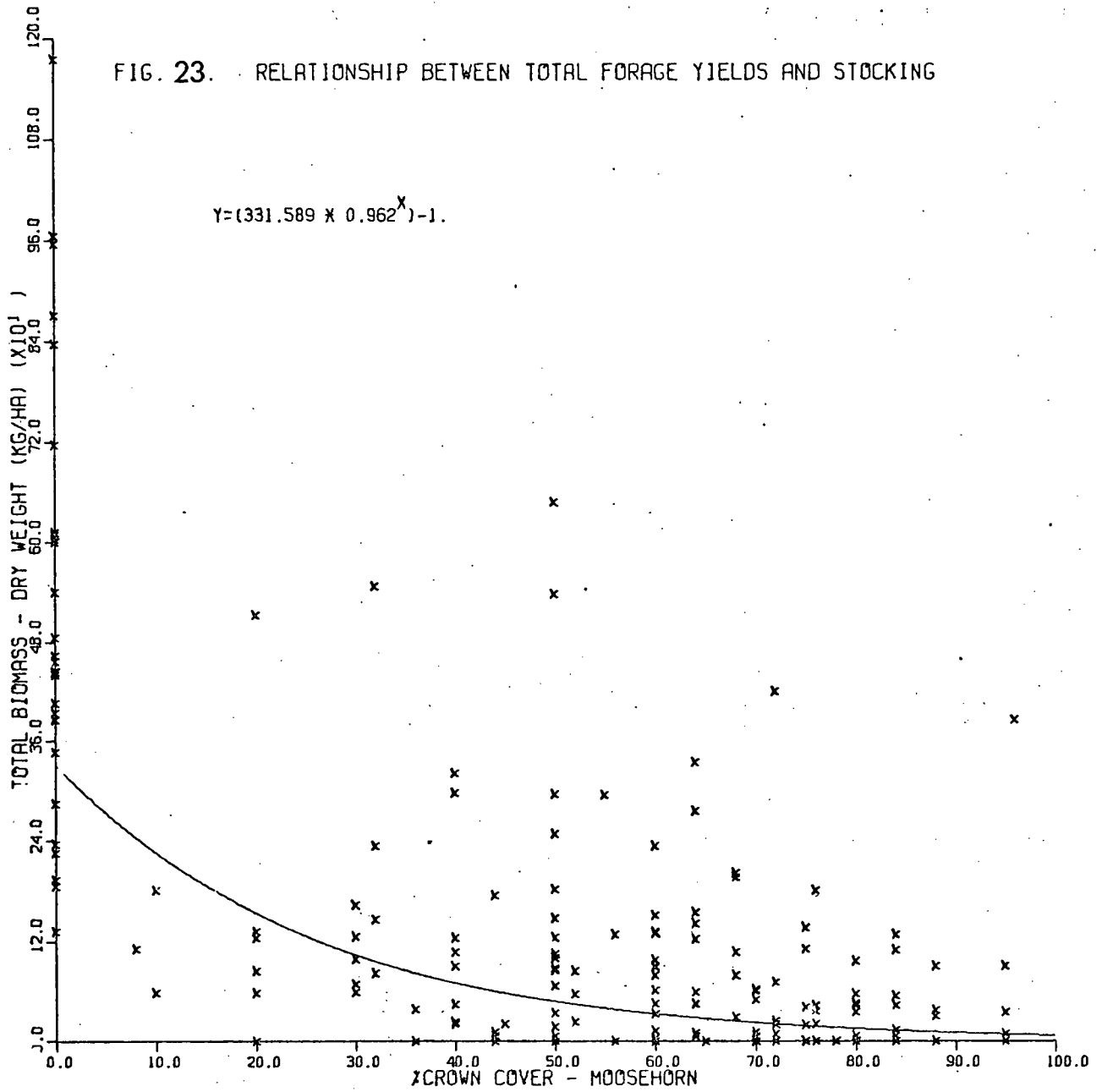
FIG. 24. RELATIONSHIP BETWEEN TOTAL FORAGE YIELDS AND STOCKING

$Y = (416.006 \times 0.958^X) - 1.$
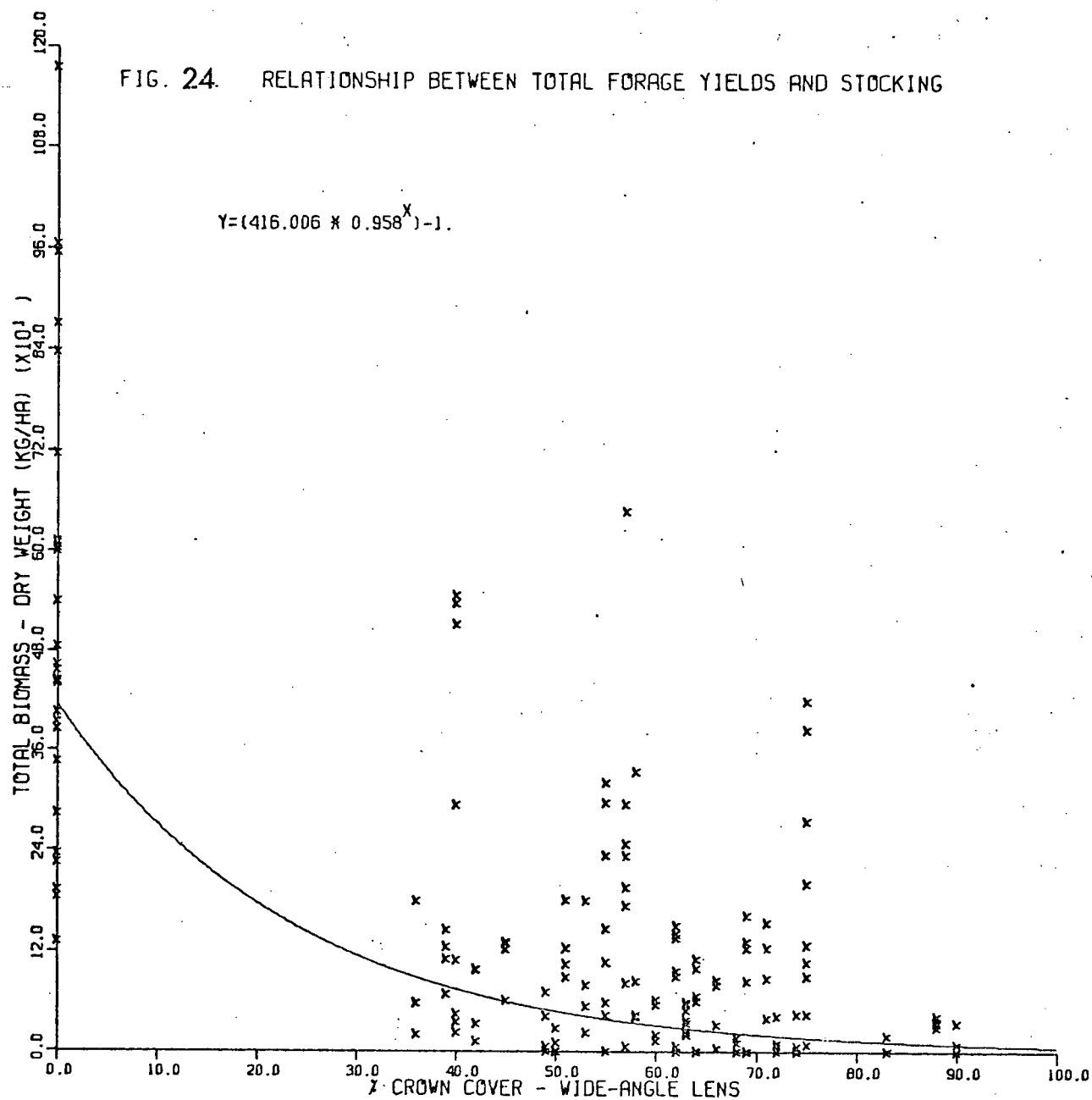
Table 12. Radial growth (.01mm) at breast height in Ponderosa pine and Douglas-fir on a medium site at Mountain view. Trees were defoliated in 1975; increment cores were extracted in winter 1976. Each average is based on 16 cores. Lw: latewood; Ew: earlywood; R: total annual ring.

	Deg.of defol:	Yr.of growth	≤15				15.1 - 25.0				25.1 - 35.0				>35				Averages			
			Lw	Ew	R	Lw/R	Lw	Ew	R	Lw/R	Lw	Ew	R	Lw/R	Lw	Ew	R	Lw/R	Lw	Ew	R	Lw/R
P$_y$	0	1975	9.8	33.0	42.8	.228	18.8	69.8	88.5	.212	14.3	46.8	61.0	.234	20.2	80.0	100.8	.206	15.9	57.4	73.3	.217
		1976	20.3	56.0	76.3	.266	22.3	64.0	86.3	.258	15.0	50.0	65.0	.231	38.0	98.5	136.5	.278	23.9	67.1	91.0	.262
DF	0	1975	30.5	66.5	97.0	.314	32.3	87.3	119.5	.270	27.3	98.5	125.3	.217	17.5	74.5	92.0	.190	26.9	81.7	108.6	.248
		1976	12.3	38.8	50.5	.243	6.8	14.5	21.3	.318	33.0	52.3	85.3	.387	8.5	23.5	32.0	.266	15.1	32.1	47.3	.320
	L	1975	9.5	25.8	35.3	.270	18.5	46.8	65.3	.284	15.3	44.8	60.0	.254	13.3	52.0	65.3	.203	14.1	42.3	56.4	.250
		1976	6.0	11.5	17.5	.343	14.0	42.5	56.5	.248	14.3	27.8	42.0	.339	11.3	43.3	54.5	.206	11.4	31.3	42.6	.267
	M	1975	20.3	57.8	78.0	.260	15.3	45.8	61.0	.250	38.8	104.5	143.3	.271	47.0	80.8	127.8	.368	30.3	72.6	102.5	.290
		1976	19.8	54.3	74.0	.267	21.5	78.3	99.8	.216	17.8	83.5	101.3	.175	29.0	95.0	124.0	.234	22.0	77.8	99.8	.221
	H	1975	36.5	80.5	117.0	.312	31.5	88.3	119.8	.263	16.0	57.0	73.0	.219	9.3	35.3	44.5	.208	23.3	65.3	88.6	.263
		1976	22.0	57.8	79.8	.276	18.5	88.0	106.5	.174	10.0	35.5	45.5	.220	6.3	22.3	28.5	.219	14.2	50.9	65.1	.218

FIG. 25. BEHAVIOUR OF EARLYWOOD WIDTH IN PONDEROSA PINE
+ REAL AVERAGE
X WEIGHTED MOVING AVERAGE ± 6 years

FIG. 26. BEHAVIOUR OF EARLYWOOD WIDTH IN DOUGLAS-FIR
+ REAL AVERAGE
x WEIGHTED MOVING AVERAGE ± 6 Years

FIG. 27. BEHAVIOUR OF LATEWOOD WIDTH IN PONDEROSA PINE

+ REAL AVERAGE
x WEIGHTED MOVING AVERAGE ± 6 years

LATEWOOD WIDTH (1.0×10⁻² mm)

FIG. 28. BEHAVIOUR OF LATEWOOD WIDTH IN DOUGLAS-FIR.
+ REAL AVERAGE
× WEIGHTED MOVING AVERAGE ± 6 years

- 64 -

FIG. 29. RING WIDTH BEHAVIOUR IN PONDEROSA PINE
+ REAL AVERAGE
× WEIGHTED MOVING AVERAGE ± 6 years

FIG. 30. RINGWIDTH BEHAVIOUR IN DOUGLAS-FIR
+ REAL AVERAGE
X WEIGHTED MOVING AVERAGE ± 6 years

FIG. 31. BEHAVIOUR OF LATEWOOD/RING IN PONDEROSA PINE
+ REAL AVERAGE
X WEIGHTED MOVING AVERAGE ± 6 years

L/R PERCENTAGE

YEAR

- 67 -

FIG. 32. BEHAVIOUR OF LATEWOOD/RING IN DOUGLAS-FIR
+ REAL AVERAGE
X WEIGHTED MOVING AVERAGE ± 6 years

more precision may be obtained by increasing the number of sample plots, instead of plot size.

Data on radial growth in trees in 1975 and following that year's defoliation are summarized in table 12. Figures 25 -- 32 inclusive represent historical radial growth at breast height in trees from the whole study area during the past century. The Douglas-fir curves are based on 150, and the Ponderosa pine curves on 79 increment cores.

Discussion

Impacts

Understory forage yields and their variability decrease with increasing stand basal area and percent crown cover. The general trends evident in the results presented here are common in the literature, but apparently mathematical models best describing forage yields vary.

Dodd (1969) found a good fit of simple linear models between percent crown cover and forage yields in "undisturbed" stands in higher elevation *P. menziesii* - *calamagrostis* association a few miles northwest of Kamloops. He admitted that curves would describe the data better. Nevertheless he applied linear models "for being more useful (sic p. 51)." Later Dodd et al. (1972) fit both linear and semi-logarithmic models on the same data and found both models significant. But because the SEE are in different units, it is not clear which form of model describes the data better.

A high linear correlation (r = 0.985) between forage yields and stocking in Ponderosa pine stands in eastern Washington was reported by McConnell and Smith (1970). Pase (1958), Jameson (1967) and others have found nonlinear relationships between yields and stand density and stocking. Gaines et al. (1954) reported a second degree parabola with "k" positive (linear: $y = b_o + b_1x + b_2x^2$) as describing forage yields on stand density: but they cautioned that the upturn in the curve might have been due to inadequacy of data. On the other hand, they correctly alluded to the possibility that the upturn might have signified a point beyond which stand density was increasing at the expense of stocking, thus making more space and light available for forage production. Jameson (1967) cited a third degree or cubic parabola (linear: $y = b_o + b_1x + b_2x^2 + b_3x^3$) as giving a best fit of his forage yields on stand density and stocking. A biological hypothesis for the shape of the continuous function is difficult to conceive. These data were obtained under in situ or undisturbed crown cover conditions. In the Southern Pine Region, herbaceous growth is also inversely related to stand density and crown closure; and forage yields are highest in openings (Blair and Brunett, 1976).

In my analyses, standard errors of the hyperbolic functions are much higher than those of logarithmic functions. Both types of models are significant. They describe the data adequately. Because of high errors associated with them, the hyperbolic models would give very wide confidence intervals if used for prediction. The logarithmic models are invariably better fitting. The coefficients of determination are misleading here because of differences in units of the dependent

variable in the two kinds of models. In their work in Montana Foothills Bunchgrass Ranges, Van Dyne et al. (1963) used coefficients of variation to conclude that grasses and forbs were less variable than shrubs. In general, Muegler (1976) concluded similarly. In my study area, grasses are most variable, and forbs more variable than shrubs. Basal area and crown cover are required to predict total forage yields well. But separate predictions of grass, forbs and shrubs require only basal area. The importance of basal area is not unexpected, as it is indicative of site quality and biological capacity. In most of the multiple regression models coefficients of determination and SEE indicate that crown cover can be ignored in predicting forage yields without necessarily losing much precision. This does not mean crown cover is not important in determining forage yields; it means basal area is more important.

Table 13 shows forage yields for two forest associations within the Interior Douglas-fir Zone. Only yields from openings are compared because of lack of stand density data in Dodd (1969), and because of possible interaction between density and stocking in this study. Williams Lake is farther north, cooler and more moist than Pass Lake. As my data are from a driest area of the three, they fall within reasonable expected ranges.

At most, 54 percent of the variation in total forage yields was due to basal area and percent crown cover. These independent variables accounted for even smaller amounts of the variation in separate yields of grass, forbs and shrubs. Likely, other factors are important in determining forage production in this ecotone. Gains et al. (1954) showed a very high correlation between grass and forb

Table 13

A comparison of forage yields (Kg/ha) from openings
in two forest associations in the Interior Douglas-
fir Zone. Data for Pass and Williams Lakes extracted
and further analysed from Dodd (1969). Data for the
other association are from six localities studied here.

| Pseudotsuga - Calamagrostis | | Pseudotsuga - P.Ponderosa - Agropyron spp. |
Pass Lake (Dry site)	Williams Lake	N. Thompson Valley - So. of Kamloops Lake
632.8	1538.8	207.8
459.4		354.3
932.5		545.4
Avges: 674.9		904.3
		484.7
		422.0
		Avge.: 486.4

yields and forest litter amounts. A thick mor forest floor may

smother vegetatively regenerating plants; it makes mineral soil

inaccessible to seeds. Severson and Kranz (1976) reported very poor

logarithmic fit of forage yield data on basal area in aspen stands.

While the yields decreased as proportion of Ponderosa pine increased,

predictability increased. They employed a double sampling technique of

ratio estimation to obtain dry weight from fresh weight of forage,

instead of drying all samples. Therefore in their regression analysis

they actually used forage yield estimates. It is not indicated, whether the error associated with the use of estimates was accounted for. It is not known whether the insignificance of their models was associated with the double sampling procedure. Notwithstanding, the authors are of the opinion that their models were insignificant because they did not tally the most important independent variable. Probably in Aspen and other vegetatively regenerating stands, "roots, total biomass or growth" are more predictive of forage yields than basal area or crown cover.

Increases of understory vegetation yields in response to tree defoliation by Douglas-fir tussock moth are evident. Greatest increases should be expected in cooler and more moist microsites in the ecotone, nearer the *Pseudotsuga calamagrostis* association and along creeks. On dry sites, where yields are ordinarily low, forage production may increase several fold, but it does not amount to much except possibly where complete defoliation results in mortality of large groups of trees. In their exploratory work, Tisdale and McLean (1957) observed forage yields under several canopies and basal area levels in several seres in the interior. They noted a pioneer aspen sere with basal area of 20.7 m^2/ha yielded an average of 270 kg/ha of forage, and the climax Douglas-fir sere with a basal area of 52.1 m^2/ha yielded only 114 kg/ha. Forage yields in transition seres of Lodgepole pine and mixed conifer/aspen were not given. In a pine stand which was killed by *Dendroctonus* beetles, probably *D. ponderosae (monticolae)*, forage yields were "... 50 percent greater than for comparable site occupied by a normal stand of *Pinus*." This appears to be the first

time an insect was recognized and documented in the literature as an

important ecological force in range management in the interior. Munro

and McT. Cowan (1947) had recognized logging and fire in this regard.

Transmissivity of insolation, and basal area in Ponderosa

pine stands are significantly related in a hyperbolic fashion (Solomon

et al., 1976). Reducing stand density provides more light to the

understory. Following defoliation, more moisture and light are available

under the canopy; and animals frequent dead patches thereby effecting

soil scarification. In one stand, two years following its death, forage

yields exceeded those in openings (Table 14; Figure 33). This also

illustrates the importance of moving shade provided by the dead trees

or snags. In adjacent undefoliated stands, forage yields were

extremely low. Not only does defoliation provide more light and

moisture to understory vegetation, it also makes available more

nutrients which leach out of the forest floor and frass. When defolia-

tion results in tree mortality, competition for these resources is

greatly reduced and understory vegetation flourishes. Dolph (1973)

gave an empirical estimate of about 7,900 animal unit months as the

magnitude of range benefits following a tussock moth outbreak in the

U.S. Pacific Northwest. From his data, it is not clear whether these

benefits are from 70.5 thousand or 80 thousand hectares. Defoliation

may have different effects on forage quality and yield. Increases in

yield do not necessarily imply increased capacity for range land. In

a black tupelo forest in the southern U.S. extensive defoliation by

the forest tent caterpillar, *Malacosoma disstria*, reduced wild game

population. This was reflected in hunters' success. Besides its

Table 14. A comparison of forage yields (kg/ha) in several plots at Mountain View. The two stands merge into each other on the same side of a main haul road, have the same slope, aspect etc. Note higher average yields (534) under dead trees and crown cover 50%; cf. average yields (485) in openings.

	Dead Stand, Defoliated 2 years before				Undefoliated Stand				Openings			
Basal area (m^2/ha)		25.3				25.3				–		
% Cr. cover	20	32	50	55	56	64	84	84				
Grass	13.6	112.6	85.4	52.2	0.0	10.0	6.6	43.1	124.0	180.0	53.2	51.5
Forbs	499.7	130.2	300.7	183.2	0.0	0.0	0.0	0.0	304.3	421.7	267.9	54.5
Shrubs	0.0	306.1	153.2	60.1	0.0	0.0	0.0	0.0	35.9	0.0	165.4	280.5
Total	513.3	548.9	539.3	295.5	0.0	10.0	6.6	43.1	464.2	601.7	486.5	386.5

Figure 33. Response of understory vegetation at Mountain View.

    a) Top: Fisheye view - Foreground: Trees defoliated
                               and dead two years ago (1974).

        Bottom: Photograph: irBackground: Negligibly defoliated.

        Bottom: Photograph from the interphase between the
                dead and undefoliated parts of the stand.

Figure 33. Response of understory vegetation at Mountain View.

b) Fisheye and ordinary views of forage response in
one plot in foreground (a, above). Forage yields
(kg/ha): $Y_g = 66.0$; $Y_f = 129.9$, under % CC 39m,
40 lens, and basal area of $20.7m^2$/ha (dead trees).

Figure 33. Response of understory vegetation at Mountain View.

    c) Top: Zone of transition between the defoliated and undefoliated parts. Note very sparse vegetation in the understory.

    d) Bottom: Understory vegetation in the undefoliated part of the stand. Forage yields (kg/ha): $Y_g = 14.9$; $Y_f = Y_s = 0.0$, under % CC = 72.0m = lens and basal area $25.3m^2/ha$.

adverse effects on the trees, defoliation encouraged growth of less
desirable brush and vines. Apparently, this caused wildlife to
abandon the devastated stands for safer ones with overstory (R.C. Morris,
1976). In the Douglas-fir tussock moth situation, the patchy nature of
infestations makes it possible for wildlife to find refuge in the general
area of an outbreak.

Because of possible recovery by some defoliated trees, the
question of stand development following defoliation is obviously
important in our attempts to determine magnitudes of the range benefits
accruing following defoliation. How much defoliation, and at what
frequency can a Douglas-fir tree continue growing or living? What is
the recovery potential of the defoliated tree? It appears we must
reduce crown cover to less than fifty percent in order to realise
geometric increases in forage yield. Eddlemann and McLean (1969)
also define fifty percent crown cover as a critical level in Ponderosa
pine stands. How long can the yield increases be maintained? In an
ecological study of fire disturbance in the southern U.S., Blair and
Brunett (1976) concluded that kind, intensity and length of intervals
(frequency) between disturbance are the most important factors in
determining stand composition. This may be true for chronically
infested Douglas-fir stands in the interior.

Let us suppose we are dealing with a stand with seventy
percent crown cover. Crown cover must be reduced to fifty percent to
realize significant increased forage yields. Also suppose crown cover
is forty-five percent following defoliation. While we needed to
reduce crown cover by more than twenty percent, all the stand requires

now is a five percent - probably two years - gain of foliage to revert

to its condition of low understory forage yields. Often we are dealing

with stands uneven in age, height, stocking and health. When these

variables are superimposed on the crown cover in our example above, it

becomes obvious that we cannot justifiably generalise about impacts of

the defoliation on forage beyond the statements made here. Moreover,

the dynamics of stand development are complex (Smith, 1974) enough

without superimposing upon them an extra ecological force.

Figure 34 is a conceptual model of forage response behaviour

in two susceptible stands. Stand a has higher density than stand b -

for simplicity, assume other factors are equal. The difference in

density is reflected in higher $\underline{in\ situ}$ forage yields in stand b,

$Y_{bo} > Y_{ao}$. Various degrees of defoliation increase forage yields to

different levels. Assume equal degrees of defoliation in both stands:

defoliation results in higher forage yields in stand b, $Y_{bi} > Y_{ai}$. At

very low degrees of defoliation, the difference in productivity between

the two stands narrows, $(Y_{b6} - Y_{a6}) < (Y_{b1} - Y_{a1})$. Following defolia-

tion, the tendency is for the stand to revert to its original state:

yield approaches the original level, $Y_{bi} \rightarrow Y_{bo}$, $Y_{ai} \rightarrow Y_{ao}$. Probably

both stands require about the same period to revert to the original

state of forage productivity; and following a low degree of defoliation,

that state would be reached in a shorter period of time than following

higher degrees of defoliations, $t_{ai} \approx t_{bi}$; $t_{b6} << t_{b2} < t_{b1}$, and

$t_{a6} << t_{a2} < t_{a1}$. Clearly, increased defoliation benefits grazing in

at least two explicit ways: by increasing yields more or less

immediately, and by sustaining the yields for a longer period.
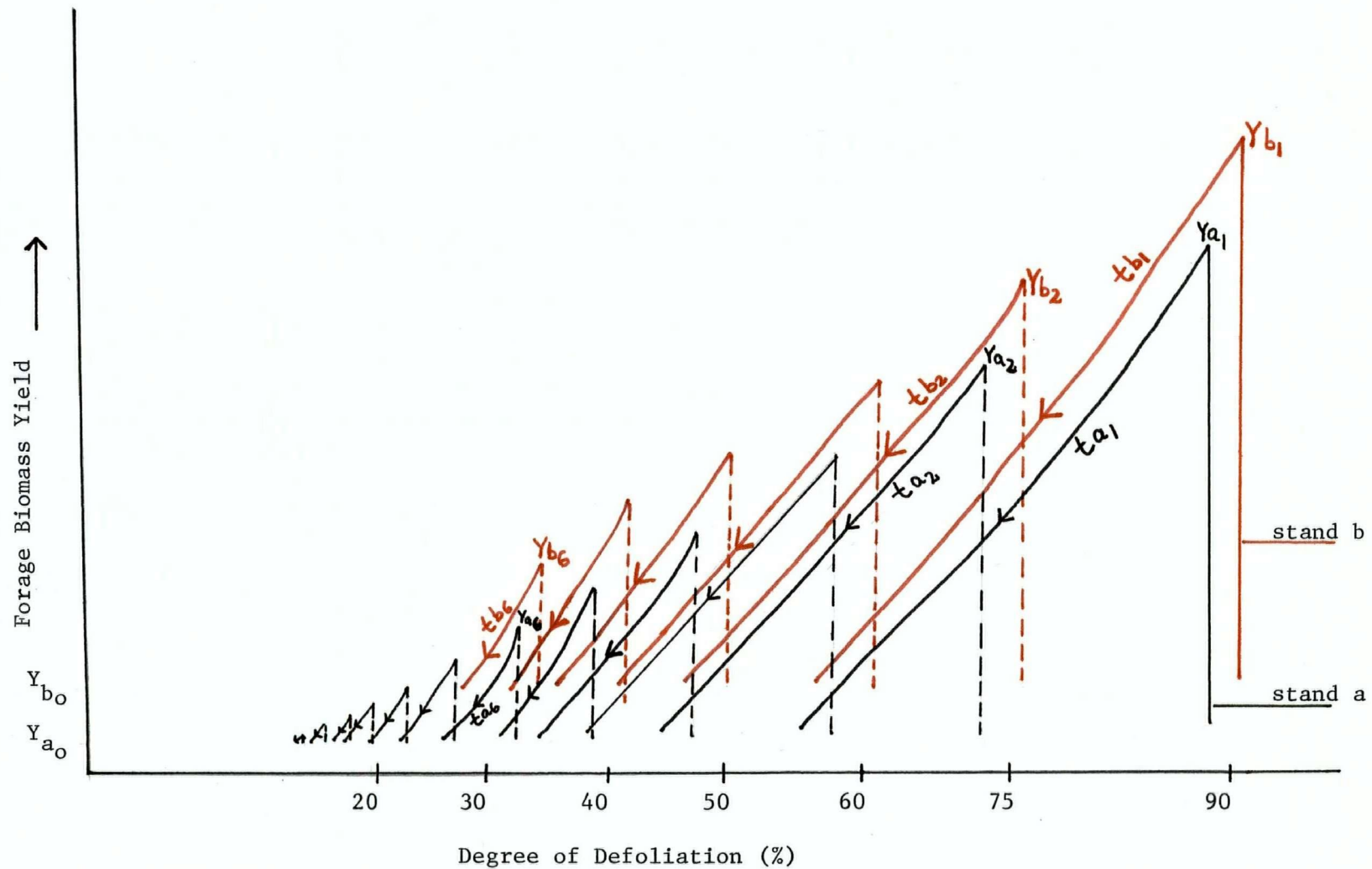
Figure 34. A conceptual model showing response behaviour of forage yields in 2
defoliated stands with different density levels.
Stand a;   Stand b. $BA_a > BA_b$; $Y_{b_o} > Y_{a_o}$

Low forage yields in, and inaccessibility of thick tree

patches (Fig. 35) to domestic and wild ungulates which are of concern

in this ecotone (McLean et al., 1970), leads one to question whether

such patches should be included in range land inventory. Criss-crossing

by dead trees fallen after their defoliation may impede accessibility,

but only to a smaller extent. Only patches occupied by dead trees and

trees seriously defoliated to the extent which requires many years to

regain suppressive crown cover represent a realistic increase in the

inventory.

In southern Alabama, Gaines et al. (1954) mentioned

individual Longleef pine trees between 18 and 36 cm dbh. influencing

grass production within a maximum distance of only 2.4 meters from the

trunk - crown widths were not given. On the other hand a group of

trees, presumably of similar size, influences grass production within a

broader zone of 9 m from the forest edge. The difference is probably

due to microclimatic influence of the forest "wall". By corollary,

following defoliation, more forage may be realized from along forest

walls than under individual open grown trees. Figure 36 shows an

impressive response of understory forage under a dead, more than 150

year-old open grown Douglas-fir tree of 86.5cm dbh and 14m crown width,

near Cherry Creek. Clearly the zone of response was delineated by the

crown. Such response reflects also a greater supply of nutrients from

frass and needles following defoliation.

Within a stand, increasing crown cover results in reduced

forage yields; but it favors grass production at the expense of forbs

and shrubs. This is true for most levels of stand density. The same

Figure 35. Top: A dense, completely defoliated plot at Dairy Creek.
            Forage yields (kg/ha): $Y = 10.0$; $Y_f = Y_s = 0.0$,
            one year following defoliation. Basal area =
            $27.6m^2$/ha; % CC = 44m, 50 lens. Forage yields
            likely to increase drastically in time if most
            trees die.

            Bottom: A dense, undefoliated plot near Cherry Creek –
            1975. Forage yields (kg/ha) $Y_t = 0.0$

Figure 36. Understory vegetation response under a defoliated,
            now dead, open grown Douglas-fir tree at Cherry Creek -
            1975.

            a. Tree Characteristics: Diameter = 86.5 cm;
                height = 26.5 m; crown width = 14 m;
                age   150 years.

Figure 36. b. Top: Close up view, in summer.

Bottom: Close up view, in winter.

Note the apparent delineation of the zone of response
by crown projection. Downy brome and Pine grass most
abundant.

conclusion is evident from examining forage composition under similar stocking levels on increasing density. Stand density and stocking, and probably other factors have an interacting effect on forage yield and composition (Table 15). At lower stocking and density levels grass is less dominant, but it still constitutes a higher porportion of biomass than forbs and shrubs.

In many cases reduction in tree growth following defoliation is considered so common that it is often assumed and used to justify insect control measures. The loss in tree production is relevant only in surviving trees; losses due to mortality may be higher. Tree form may be impared by top kill and formation of spikes, bayonets and forks. This is significant in young stands. In 1973 extensive top kill in a forty one hectare stand near Osoyoos was noted in a Forest Insect and Disease Survey Annual Report.

Defoliation may reduce photosynthetic surface enough to affect tree growth. Theoretically, serious reduction in tree growth should be expected because the tussock moth defoliates from above, where current year needles and their biomass are concentrated (Silver, 1962; Smith, 1970). Gordon (1962) studied competitive effects of common understory species on tree radial growth in the "east side pine type" in California. Removal of bunchgrass resulted in increased radial growth in widely scattered Ponderosa and Jeffrey pine trees. Possibly, in my study area, increased productivity of understory forage following defoliation may prevent residual trees from realising significant growth increment. In his analysis of 4 dominant and codominant coastal Douglas-fir trees, Silver (1962) found the current

Table 15. Percent forage composition under crown cover, by stand density classes. Crown cover classes: 1: 0-10% (mostly openings); 2: 11-30%; 3: 31-70%; 4: >71%. Maximum CC = 95% for moosehorn, 90% for wide angle lens. - indicates no plots obtained in treatment. Data from 172 plots.

| | Basal Area Class (m^2/ha) | | | | | | | | | | | | | | | |
| | 0 - 11.5 | | | | 11.6 - 23.0 | | | | 23.1 - 34.4 | | | | 34.5 - 50.0 | | | |
Crown cover class	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Moosehorn																
Grass	40	-	-	-	-	3	51	49	-	100	87	83	-	-	96	92
Forbs	28	-	-	-	-	97	27	8	-	0	13	7	-	-	<1	4
Shrubs	32	-	-	-	-	0	22	43	-	0	0	10	-	-	4	4
Wide angle lens																
Grass	40	-	-	-	-	-	49	67	-	-	84	100	-	-	91	21
Forbs	38	-	-	-	-	-	30	17	-	-	11	0	-	-	9	4
Shrubs	32	-	-	-	-	-	21	16	-	-	5	0	-	-	0	75

year foliage in the upper 1/3 amounted to over 12 percent more than in the lower 2/3. The current year foliage is preferred food by the tussock moth (Beckwith, 1976). Further analysis of Silver's data shows there are more needles per linear 2.5 cm (1 inch) of foliated twigs in the lower 2/3:

Tree number

	1	2	3	4
	No. of needles per linear 2.5cm.			
Top 1/3:	261	230	229	257
Bottom 2/3:	290	161	299	273

This implies more dilution of current year foliage in the lower parts of the crown; a higher concentration provides a better chance for the insect to locate good food in the upper crown.

We may suppose that weather and both forage and tree growth are related; but McLean and Smith (1973) were unable to find significant correlation between forage yields and tree ring growth. The high variation in yields and ring width behaviour is attributed to local conditions or microsite. We may assume that weather directly affects the tussock moth as well as tree growth. The insect also affects trees so that the impact on tree growth is likely a summation of at least climate and defoliation. Trees affect the insect in a feedback fashion:
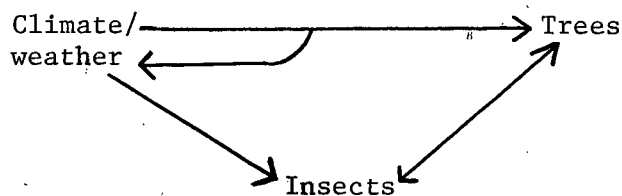
As Koerber and Wickman (1970) emphasized, an outbreak may only magnify the impact of the weather if the weather correlated with the outbreaks retards tree growth.

The Duff and Nolan (1953) concept is not helpful in isolating impacts of several extrinsic or "environmental" factors such as insects and weather. So I examined impacts on tree growth by analysing ring growth behaviour in Ponderosa pine and undefoliated Douglas-fir trees, as controls, and in trees defoliated to different degrees.

Various workers have examined tree growth following silvicultural treatments such as pruning, thinning and fertilization, and following natural and man-made disasters of defoliation. Effects of pruning were examined in Douglas-fir by Stein (1955) and Staebler (1963; 1964). Pruning from below up to 25 percent of the live crown increased diameter growth at breast height, indicating the pruned branches were a burden to the tree. Increased severity of pruning almost invariably reduces growth. In Lodgepole pine defoliated by the Lodgepole needleminer, *Coleotechnites (Evagora) starki,* reduction of radial increment is immediately evident in upper parts of the stem, but there is a two year lag at breast height (Stark and Cook, 1957). For Grand fir, Douglas-fir and Engelmann Spruce defoliated by western Spruce budworm, *Choristeneura occidenetalis,* C.B. Williams (1967) found parts of the stem near the ground were more "complacent" in exhibiting reduction than parts higher up. Douglas-fir showed the least reduction.

Although generally tree growth is directly proportional to amount of foliage present (Mitchell, 1975), it is necessary to evaluate the feeding behaviour of a defoliator, and the needle crop distribution the crown configuration and

within the crown configuration in order to postulate some theoretical
expectations for impacts of defoliation. Radial growth impacts
include missing and discontinuous rings (O'Neal, 1962; 1963), immediate
and delayed reduction in ring width, no response and increased ring
width (Staebler, 1963; Polge and Garros, 1971). Polge and Garros
explained the increase as due to mobilization of stored food in
parenchyma. But cambial activity (and hyperactivity) is due to growth
regulators rather than stored carbohydrates (Kozlowski, 1969). Webb
and Kilpatrick (1976) found significant reduction in starch content in
Douglas-fir trees defoliated by the tussock moth near my study area.
K. Graham (1963) was of the opinion that increased radial growth is likely
due to lower rates of transpiration and translocation following
defoliation. Except in extreme cases, temperature in the stem is
unlikely to increase fast enough to negate the increase in growth by
promoting faster rates of metabolism.

Since growth in Douglas-fir is determinate, and since in this
species most photosynthates are stored in buds and needles, effects of
defoliation in one year should not be evident in earlywood the following
year. Effects should, however, be evident in latewood because its
formation largely depends on current year photosysthates. Tables 16
and 17 summarize data of tree radial growth at breast height in 1976
at Mountain View. Defoliation occurred there in 1975. I have attempted
to use 1974 and 1975 radial growth in defoliated Douglas-fir trees, and
1976 growth in undefoliated trees as controls in examining possible
reduction in radial growth at breast height following defoliation.

Ponderosa pine gained more radial increment in 1976 than in

Table 16. Average percent change in tree radial growth at breast height following defoliation at Mountain View in 1975.

Top: Growth in 1976 as percent change from 1975 growth in the same trees.
Bottom: 1976 growth in defoliated trees as percent of 1976 growth in undefoliated Douglas-fir trees.

	Ponderosa pine	Douglas-fir			
Deg. of defoliation:	0	0	Low	Medium	High
Lw	+50	−44	−19	−27	−39
Ew	+17	−61	−26	+ 8	−22
Ring	+24	−57	−25	− 3	−27
Lw/Ring	+21	+29	+ 7	−25	−17
Lw			76	146	94
Ew			98	242	155
Ring			90	211	138

Lw: latewood;   Ew: earlywood.   Data are based on 16 cores in each class.

Table 17. Average percent change in tree radial growth at breast height by tree size, following defoliation in 1975 at Mountain View. Growth in 1976 as:

Top: Percent change from 1975 growth in the same trees;
Bottom: Percent change from 1974 growth in the same trees.

	Deg. of tree defol.	Diameter class (cm)											
		≤15			15.1 - 25.0			25.1 - 35.0			>35		
		Lw	Ew	R	Lw	Ew	R	Lw	Ew	R	Lw	Ew	R
P_y	0	+107	+70	+78	+19	- 8	- 3	+ 5	+ 7	+ 7	+ 83	+23	+35
DF	0	- 60	-42	-50	-79	-83	-82	+21	-47	-32	- 51	-69	-65
	L	- 37	-55	-50	-32	- 9	-14	- 7	-38	-30	- 15	-17	-17
	M	- 3	- 6	-0.2	+41	+70	+64	-54	-20	-29	- 38	+ 5	- 3
	H	- 40	-28	-32	+41	-0.03	-11	-38	-38	-38	- 32	-37	-36
P_y	0	+178	+79	+98	+29	- 6	+0.4	+ 7	-20	-15	+111	+42	+56
DF	0	-60	-51	-53	-67	-82	-79	- 2	-33	-24	- 36	-58	-53
	L	-20	-14	-46	+ 2	-16	-12	0	-27	-20	+ 8	-20	-17
	M	+ 8	-12	- 8	+62	+21	+28	-57	+11	-13	+ 2	+30	+22
	H	-20	-18	-19	- 8	-0.2	- 1	-47	-31	-35	- 51	-44	-46

Lw: Latewood; Ew: earlywood; R: Total annual ring.
Data are based on 4 cores in each class.

1975. The opposite is true for sympatric Douglas-fir. In defoliated trees, within the first year, reduction in radial growth was less than in undefoliated Douglas-fir trees. The reduction is apparently not correlated with tree size. Defoliation seems to have retarded immediate growth reduction. Evidently at breast height, there is a lag of more than one year in Douglas-fir growth following defoliation. Impacts at breast height may be more dramatic in characteristics other than radial growth. It may be speculated that defoliation early in the growing season results in nutrients being rechannelled from branch tips to the trunk.

In the past century, trees in the study area experienced two periods of good growth and three of poor growth (Figures 25 to 32, inclusive). These graphs and significant correlation coefficients of 0.6, 0.8, 0.7 for earlywood, latewood and ring width of Douglas-fir and Ponderosa pine indicate that the two species experienced similar radial growth trends. Generally, Douglas-fir grew faster than Ponderosa pine trees. But during periods of depression, growth of Douglas-fir was reduced more than Ponderosa pine.

Superimposing North Thompson and Kamloops historical outbreaks (Figure 1) on the radial growth behaviour graphs, it is noteworthy that three outbreaks occurred during low growth periods (depressions) and one during a semifavorable period. A depression may accommodate more than one outbreak. Because we know nothing about the specific outbreak history of these trees, we cannot state whether or not defoliation played a role in the growth depressions. It is not even known if the outbreaks occurred in the general vicinity. Some

growth depressions precede the beginning of outbreaks, indicating that growth reduction in Douglas-fir is not necessarily a result of outbreaks.

Probably some common factor(s) affects radial growth behaviour in the two species. The factor is probably a macro one since trees used in this historical analysis are from a wide area. The coincidence of some outbreaks with depressions in tree growth suggests a similar factor also affects insect populations. But apparent inconsistency in the coincidence suggests a macro factor is not the only important one. The overall factor may set the stage within which several cofactors function to determine insect population trends. More conclusive statements cannot be made from this analysis without the risk of making tenuous assumptions. A knowledge of history of the trees or stands studied here would have made this part of the project more than exploratory. The difficulties of assigning cause-effect relationships when enough information is not known are evident in the following chart.

Probably the most spectacular impact of Douglas-fir tussock moth outbreaks is the sometimes extensive, visually obvious tree mortality they inflict on the landscape. In Forest Insect Disease Survey records, reports of extensive mortality near Vernon were recorded in the following years: 1921-1922, 1929-1930, 1938-1939, and 1945. Mortality near Chase, Armstrong, Hedley and other places was noted in various years. Many workers in the U.S. also have expressed concern about the destructive power of the Douglas-fir tussock moth. D.A. Graham (1974) stated that the insect can cause mortality one year following defoliation in unnamed host, and contrasted

Is radial growth behaviour in DF correlated with Py?

Yes →

No →

The two species respond similarly to the same or different factors

Lack of correlation may be due to high variability in the population: Regroup trees into smaller populations or increase sampling intensity

Does ring width coincide with outbreak periods

Yes ←   No →

Is behaviour now consistent?

Yes ←   No →

Is the coincidence consistent

Yes ←   No →

Working hypothesis: Radial growth behaviour and insect populations are determined by, or respond differently to the same or different ecological factors

Trees are complecent: Possibly the hypothesized interaction between climate, trees and insects may be valid Impacts may be in terms of other than radial growth behaviour.

Working hypothesis: Radial growth behaviour and outbreaks likely respond to a common ecological factor(s)

Other factors play important roles in outbreak occurrence

?

?

?

?

95

this with Balsam fir which can tolerate as many as three consecutive years of defoliation by spruce budworm.

In 1949, a Forest Insect and Disease Survey report noted that in Monte Creek and Duck Ranger Districts, defoliated trees between 35.5 and 40.6 cm dbh were also attacked and killed by the Douglas-fir beetle, *Dendroctonus pseudotsugae*. In western U.S.A., a range of mortality from 66 percent to 95 percent has been attributed to bark beetles in tussock moth defoliated stands (Wickman, 1958; 1963; Wickman et al., 1973; D.A. Graham, 1974; Carolin and Coulter, 1975). Size "preference" by the beetles was not indicated in the FIDS reports; but it was evident in my study area (Figure 37). The 1949 Forest Insect and Disease report also suggested that Douglas-fir is highly resilient to tussock moth defoliation. It stated that all (Ponderosa) pines which had been defoliated, presumably by the tussock moth, were dead in contrast to Douglas-fir which recovered quickly. A 1964 Forest Insect and Disease report: "... (Douglas-fir) trees which were almost denuded (of foliage) in 1963 grew a surprising amount of foliage." More recently, Carolin and Coulter (1975) have shown that in the U.S. Pacific Northwest, Grand fir is damaged more than Douglas-fir even when insect density is equal in the upper 1/3 of the crown in both species. The authors did not speculate on possible reasons for this difference. Is it due to certain differences in lengths of time needle crops are retained on the two species, or to differences in foliage (age) distribution in their crowns? Wright (1974) had observed that actually the greater damage to Grand fir stands was due to differential defoliation by the tussock moth. But to state, as he did, without

Figure 37. Some defoliated Dougl-

Figure 37. Some defoliated Douglas-fir trees infested
with bark beetles. Size preference evident.
Note thriving Ponderosa pine.

further comment that susceptibility increased with Douglas-fir component

in the Blue Mountains seems contradictory, and serves to confuse the

situation.

The question of what level of acute or chronic defoliation

is necessary before Douglas-fir trees succumb is relevant in assessing

mortality impacts more precisely. In the Pacific Northwest, fifty

percent defoliation was indicated to be the threshold in unnamed species

Figure 38. Lush current year needle crop on small Douglas-fir
            trees, following complete defoliation during the
            previous year. Evidence of good recovery unless
            redefoliated!

            Top; middle: Cherry Creek,

            Bottom: Indian Gardens

U.S.D.A., 1973b). I did not embark on an estimation of a threshold

because of difficulties involved in estimating defoliation levels

precisely. Instead, I examined recovery of Douglas-fir trees which

had been completely defoliated in the preceding year. Color and

position of current year needles facilitated my classifying a tree in

this category. Good recovery rates are evident in small trees

(Figure 38), and mortality is most serious only among large trees

(Tables 18, 19, 20).

Table 18

Recovery of completely defoliated trees in a stand at
Heffley Creek hillside (M-site quality), and dynamics
of their growth. Data are based on 170 trees from 2
representative strips. Trees were tallied one year
following defoliation.

| | | | Diameter class (cm) | | |
	<5.0	5.1-10.0	10.1-15.0	15.1-20.0	20.1-25.0
% Survival	76	72	80	66	50
Avge diam (cm)	2.8	7.1	11.4	17.5	23.1
Avge height (m)	2.6	7.0	10.6	13.4	16.5
Avge Cr. length (m)	1.5	3.8	4.4	5.4	6.0
Avge Cr. width (m)	1.3	2.3	3.4	4.6	5.5
Diam/Cr. lgth	1.9	2.0	2.6	3.2	3.9
Diam/Cr. width	2.2	3.1	3.4	3.8	4.2
Ht/Cr. lgth	1.7	1.8	2.4	2.5	2.8
Ht/Cr. wdth	2.0	3.0	3.1	2.9	3.0

Table 19

Recovery of completely defoliated trees on a southeast
facing dry site, and dynamics of their growth. Data
are based on 158 trees - residuals from salvage logging.
Trees were tallied one year following defoliation.

| | Diameter class (cm) | | | | |
	<5.0	5.1-10.0	10.1-15.0	15.1-20.0	20.1-25.0
% Survival	76	68	76	82	66
Avge diam (cm)	3.1	7.6	12.5	17.3	20.8
Avge height (m)	3.0	8.3	11.7	13.4	16.7
Avge Cr. length (m)	1.6	3.3	6.1	8.2	8.3
Avge Cr. wdth (m)	1.3	1.7	2.3	2.7	3.4
Diam/Cr. lgth	1.9	2.0	2.1	2.1	2.5
Diam/Cr. wdth	2.4	4.5	5.4	6.4	6.1
Ht/Cr. lgth	1.9	2.2	1.9	1.6	2.0
Ht/Cr. wdth	2.3	4.9	5.1	5.0	4.9

Table 20

Survival of all, completely defoliated Douglas-fir trees
tallied in the study. Data are based on 466 trees from most
plots and strips in the study area. Trees were tallied
one year following defoliation.

| | Diameter class (cm) | | | | | |
	<5.0	5.1-10.0	10.1-15.0	15.1-20.0	21.1-25.0	>25.1
Trees tallied	152	136	109	44	17	8
Trees living	113	98	79	37	12	4
% Survival	74	71	64	84	71	50

Apparently, the larger the tree the lower the chances of recovery as levels of defoliation increases. Older stands traditionally have low stocking levels; increased mortality following defoliation further reduces stocking to lower levels. This is advantageous from the point of view of graziers as increased understory forage yields may be realized.

The ratio of dbh/crown length or width increases with tree size, indicating the crown becomes relatively smaller. The ratio is higher on drier and poorer sites, where a smaller crown may serve to minimize evapotranspiration.

In many stands in the ecotone, trees are widely spaced so that competition seems insignificant. The chance of some trees being released following defoliation of others is remote, except in a few thick patches. Vincent (1962) observed release of Balsam firs in stands infested with Spruce budworm in the well known Green River Watershed in New Brunswick. He thought the evidently slow release of advance Balsam fir regeneration was due to more light penetrating through, and reduction of competition following defoliation. Advance Douglas-fir regeneration is not immune to defoliation by the tussock moth, but most of it recovers well.

Harwood (1975) was of the opinion that severe Douglas-fir defoliation affects cone bearing trees and seed production for some time. Vincent (1962) also alluded to the need for seed availability immediately prior to defoliation for successful natural regeneration in Black spruce stands. In the study area, under dense stands and high crown cover tree regeneration was uncommon. The denseness of

these patches made them inaccessible to ungulates. The forest floor
and litter layer remained undisturbed and thick. Reduction of stocking
and density by defoliation would make stands accessible to ungulates.
Scarification effects should be evident in increased forage yields and
regeneration. In protected openings, high stocking of Douglas-fir
regeneration was common. Ponderosa pine regeneration was very scarce
even when cones were clearly abundant on the ground (Table 21, Figure
39). Whether the Ponderosa pine seeds were eaten by mice and squirrels

Table 21

Average regeneration stocking in experimental plots
under canopy and in adjacent protected openings.
Averages are based on 4 plots under canopy, and between
4 and 10 plots in openings. Only the 8 tree plots out
of 36 had regeneration.

| Basal area (m^2/ha) | Regeneration stocking (No./m^2) | | | | |
| | Tree plot | | | Adjacent protected opening | |
	$\%CC_{moose}$	F	Py	F	Py
13.8	39	2.0	–	0.0	–
16.0	64	1.5	–	2.5	–
16.0	63	0.5	–	7.6	–
18.4	69	0.5	–	1.3	–
20.7	42	5.0	–	7.4	2.0
23.0	36	3.3	–	5.1	–
25.3	64	0.5	–	7.8	–
41.3	51	2.5	–	3.0	–

Figure 39.   Abundance of cones on the ground; but no
regeneration was evident in some openings.
Behind the range pole is undefoliated plot.
Forage yields (kg/ha): $Y_t = 51.6$; $\%CC = 67_m$,
67_m, 64_{lens}.   Cherry Creek, 1974.

more than were Douglas-fir seeds, or whether there were differences in

seed viability between the two species is not known. The low

regeneration stocking under high crown cover regardless of the stand

density implies that light is limiting for Douglas-fir regeneration

in the ecotone. For adequate natural regeneration, seed availability

prior to defoliation appears necessary.

Salvaging dead or dying trees reduces loss of timber volume and value. Unlike the process of salvaging bark beetle infested trees salvaging tussock moth killed trees does not drain insect numbers from infested stands. It may in fact serve as a means of dispersal for the insect if salvaging is carried out during the summer months.

The ability to salvage is constrained by size and pattern of an outbreak, which in turn affect economics of harvesting. Except in second growth, accessibility is a costly problem especially for the small (gypo) operator. The age and size of infested stands, and of dead trees also determine the feasibility of salvaging. In California, extensive outbreaks in true fir stands often result in a race against *Scolytus* and *Tetropium* beetles, and decay. Hidden defects of wetwood (Wickman and Scharpf, 1972) are also important. In a California study, 81 percent of topkilled trees had wetwood along the whole tree compared to only 2 percent in uninfested stands. Wetwood reduces timber quality, as it leads to excessive checking and collapse, and gluing difficulties due to uneven distribution of moisture at equilibrium following drying. The race against time also is serious when logging is restricted to certain times of the year, due to excessive snow, wet ground or other reasons. In my study area, if salvaging were restricted to dead trees or patches harvesting costs would probably be prohibitive unless those people who benefit from increased forage yield contributed. Quality of dead Douglas-fir trees is probably not impaired within the first year following defoliation. Most of the logging in devastated stands is selective inasmuch as only trees larger than economic marginal size are removed (Table 22;

Figure 40). The stand structure is consequently changed.

Many large undefoliated Ponderosa pine trees are removed together with Douglas-fir trees for economic reasons. As much as 16 percent of the volume removed from several settings by an operator was "mix". Utilization stands were quite low. A cruise in stands adjacent to a setting indicated a gross volume of $178m^2$/ha. From a volume/ weight ratio, Balco Industries, a local firm estimated as having extracted only $31m^3$/ha, or about 20 percent of the volume. Such yields are due to low-poor site quality, possibly stand immaturity and the fact that only salvageable material was removed.

Experienced cattlemen were of the stern opinion that skidding or tractor logging serves to scarify the soil, and is beneficial because this is likely to increase forage yields even without range seeding.

Table 22

Stand composition of Douglas-fir trees in defoliated
stands before and following salvage logging. Data
are from 4 representative strips near Heffley Creek.

	<5.0	5.1-10.0	Diameter class (cm) 10.1-15.0	15.1-20.0	20.1-25.0	>25
			Percentage of trees in class			
Before logging	6	25	25	23	2	19
Following logging	26	34	31	7	2	0

Figure 40. Structure of residual stands following salvage logging.
Marginal tree size Ca. 20 cm.

Top: Heffley Creek, public property.

Bottom: Mountain View, private property (Mr. Inskip).
Logging progressing into the devastated area.

Salvaging may have impacts on the bird community. Birds of the primitive coniferous forest are almost all insectivorous. Removal of the forest enhances establishment of mountain and western bluebirds and other graminivorous birds, many of which prefer inhabiting coniferous forest - grassland ecotones (Thomas and McCluskey, 1974). They are mostly cavity nesters, and heavy herbaceous flora provides desirable cover. To the extent that snags may be critical for survival of these birds, care should be taken during salvaging to preserve some dead trees.

Some insects may have a serious negative impact on bird populations as much as birds have on the insects. Defoliation may expose bird nests to the extent where insolation may be lethal to nestlings, and may lead parent birds to abandon their pregeny. This impact was mentioned in a Gypsy moth, *Lymantria (Porthetria) dispar*, outbreak in eastern U.S.A. (Commonwealth of Massachussetts, 1908). K. Graham (1963, p. 251) refers to some European literature on this impact.

Epidemiology

Regulation of insect numbers reflects, in part, an impact of the insects on themselves. Knowledge of insect epidemiology enables economic entomologists to forecast trends of insect populations, and future damage so that appropriate action may be taken. The knowledge is necessary for formulating rational pest control policies and strategies.

Life cycle and sexual dimorphism of the Douglas-fir tussock moth have already been mentioned in a previous section. Several studies have been undertaken in examining aspects of population dynamics of this insect. The cyclical nature of outbreaks in several locations is quite striking. So is the synchronous nature of outbreaks between locations over a wide latitudinal range from New Mexico to Kamloops. This distribution in time and space, and the wingless nature of ♀ adults make it unlikely for these populations to be related[4] genetically. For populations which are close to each other, inability of the ♀♀ to fly reduces frequency of gene flow between them. Genetic relationship would require consistent dispersal of ♂♂, which is highly unlikely for populations farther apart than 2500 km - between New Mexico and Kamloops! Evidence indicates most populations are "independent" of each other. Even within a stand, growth of one population is not necessarily related to trends in another population. Mason (1974) has shown this in fifty plots in a 121ha stand. He employed R.F. Morris's (1963) analysis of Trend Index [$I = N_t/N_{t-1}$] and concluded that for populations within a stand, the first, second and third year, the trend indices were 7, 3, <1 respectively. He also showed in a dynamic population model, $N_t = f$ (density), that more than 80 percent of the changes in numbers during one year were due to changes in the same population during the preceding year. This meant that contagion was insignificant or immigration equaled emigration in numbers and quality.

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[4] Dr. R.R. Mason, For. Sc. Lab., Corvallis, Oregon, U.S.A. Concurs with this view in personal correspondence.

In spite of the fact that dependence has not been demonstrated, views implying it exists are not uncommon in the popular literature. Opinions such as "... the tussock moth can just eat its way to those firs on our coast,"[5] and "... District Forest Ranger said the (Douglas-fir tussock) moths were travelling toward a large stand of virgin timber..."[6] are ill founded. They represent a misunderstanding of an important issue. We know the tussock moth does not swarm like locusts! The historical frequency of the tussock moth on the coast is negligible. In fact the insect may have never inhabited much of the coast. Unfortunately the alarmist views sometimes serve the purpose of marshaling public support and sympathy for what would otherwise be unjustifiable control measures. Livingstone and Tunnock (1973) were convinced that surveys clearly showed great potential for the insect to spread. It is not clear whether they were worried about devastation of susceptible stands by autochthonus or "migrating" insects. Despite this ambiguity, the belief was used in an argument in attempts to persuade the U.S. Environmental Protection Agency to grant permission for the latest D.D.T. aerial spray in the Pacific Northwest (see U.S.D.A. 1973b).

In Western U.S.A., where the tussock moth has been intensively studied, three population phases, viz. release→peak→decline are so commonly referred to as to suggest they are a constant feature of the insect. The idea and terminology appear to have originated from

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[5] The Oregonian. 3rd November, 1972.

[6] The Oregon Journal. 18th July, 1947. (Courtesy of Dr. R.R. Mason, personal correspondence).

Greenbank (1963) in his work with eastern Spruce budworm. Most tussock moth infestations are recorded as lasting three years (U.S.D.A., 1973a) - hence the so called three year cycle. Wickman et al. (1973) ascertained the cycle in five separate case studies. Each phase is considered to last one year. This time dimension may serve to warn resource managers about the state of an outbreak, but it is not likely representative of all populations. The preparatory (release) phase probably lasts longer than one year. It is difficult to define what constitutes a release phase because the very low population levels imply difficulties of detecting the insect. A "shotgun effect" (Figure 41) so common on infested landscape suggests the three year cycle may be unrealistic. It is evident in Figure 1 that outbreaks may last for as long as five years. As D.A. Graham (1974) pointed out, in one infested patch the cycle may be a three year one, but it may be longer in a stand or forest with several patches. The infestation patch we see up the hill is not necessarily in the same phase as the one down the valley.

The quasisynchronous occurrence of outbreaks over great distances leads one to suggest that some regional factor determines, at least in part, the outbreaks. If this were true one would suspect effects of the same factor to be expressed in other organisms. If this subsidiary postulate were shown to be true, it would lend credence to the principal hypothesis. Rejection is not "derogatory" to the primary hypothesis, however (Peddie, 1938). This area is examined through tree ring analyses reported elsewhere in this thesis.

The Douglas-fir tussock moth is a "hitchhicker" (Wolfenbarger,
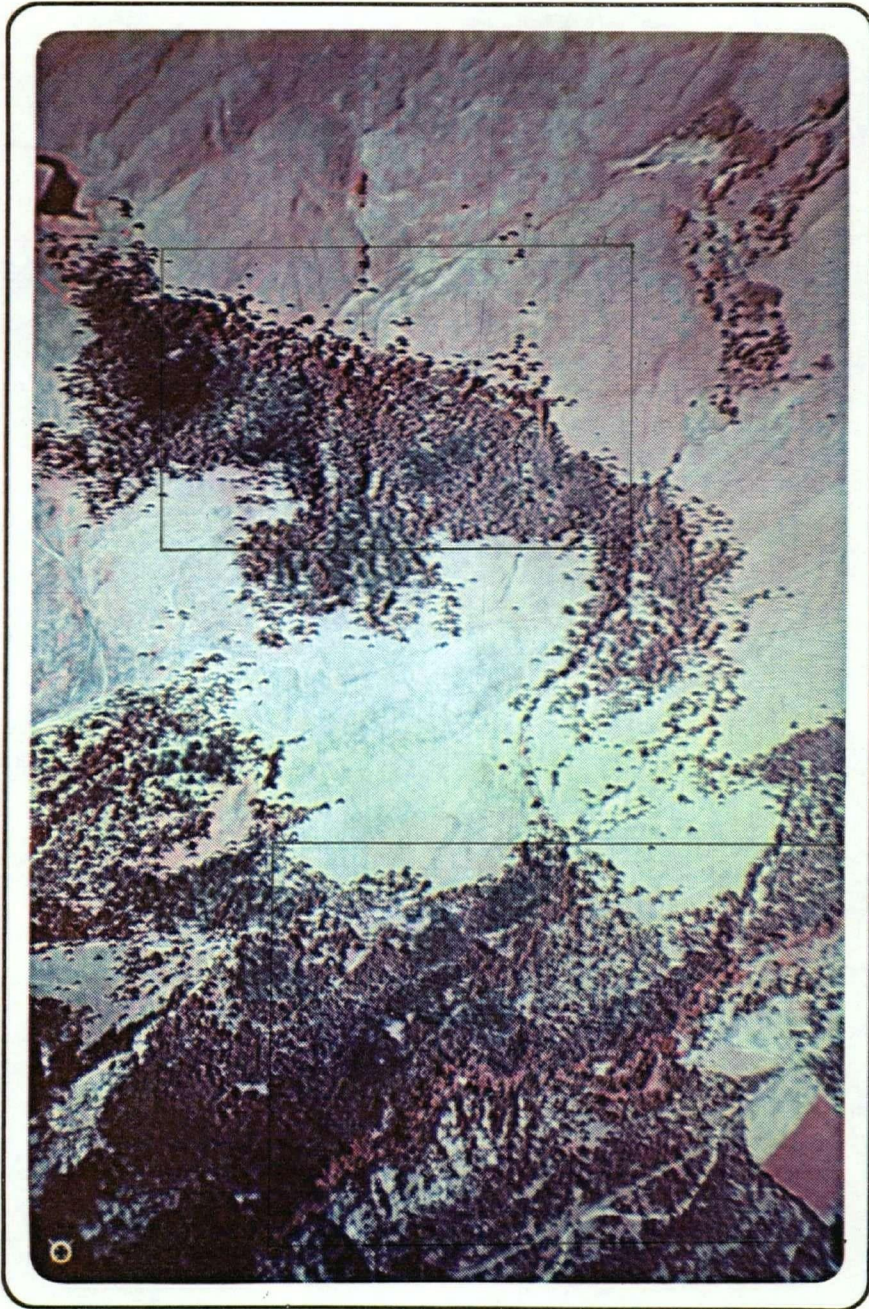
Figure 41.   Shotgun effect: typical nature of Douglas-fir
             tussock moth infestation on a landscape.

1946) on people, animals, automobiles and in wind, in the larval stage.
Probably mortality is high in the transportation medium unless travel
is restricted to the terrestrial zone (Berland, 1935), or active
plankton zone (Wellington, 1945) - more than 2 km above ground and 7°C.

The reciprocal influence of trees on the tussock moth
indicated in the interaction triangle on page 88 is real. It
represents "resistance" or feedback common between living systems.
I have encountered in the literature two sets of data which although
not intended to illustrate this concept, illustrate it well in the
tussock moth situation. Condrashoff and Grant (1962) reported their
survey on distribution of diapause sites (larval coccoons) in stands
defoliated by the tussock moth near Vernon, B.C. In a stand with
trees denuded of their foliage, the understory vegetation is favored
for oviposition sites; Douglas-fir regeneration being the preferred
plants. Number of cocoons on the reproduction averaged more than
twice the number on Choke cherry and Douglas maple combined. In a
stand where the overstory is completely defoliated, emerging larvae
immediately feed on the reproduction. The distribution of cocoons
within a Douglas-fir tree varies with the degree to which the tree was
defoliated (Table 23). In general, Luck and Dahlsten (1967) and
Dahlsten et al. (1970) concluded similarly for cocoon distribution in
White fir. Heavier defoliation results in a shift in relative
"preference" of the insects for the bark and lower parts of the tree
as oviposition and refuge sites. On these sites and on the favored
understory vegetation, probably predation and other mortality factors
are more intense. The distribution also illustrates the need for

Table 23

Distribution of Douglas-fir tussock moth cocoons in
lightly and heavily defoliated trees. (Modified from
Condrashoff and Grant, 1962).

	Crown stratum			Bark
	Upper	Middle	Lower	
Degree of defoliation				
Light	189	74	80	16
Heavy	156	196	223	139

stratifying the sampling design along the vertical axis for purposes
of sampling tussock moth populations. Also it is necessary to change
the intensity of sampling in various parts of the crown and tree as
the degree of defoliation changes.

By enhancing air circulation and formation of thermals in
the forest, intensive defoliation by the tussock moth promotes its
chances for dispersal. This improves the chances of survival for both
emigrants and residuals when food is still available. But this may
also reduce the residual populations to a point where biotic agents can
bring them down, especially when stress is prevalent in the residuals.
Current year needles are eaten first during the release phase. During
peak and decline phases only older needles which probably have lower
food quality are available. Beckwith (1976) free-fed and force-fed

tussock moth larvae on foliage from different crown strata of three
hosts. I tabulate his data to illustrate a reciprocal impact:

Host	Source of foliage	% Survival	
		*Free feeding	*Forced feeding
Douglas-fir	Top	100	100
	Bottom	100	100
Grand fir	Top	100	100
	Bottom	100	90
Subalpine fir	Top	90	80
	Bottom	100	70

*Free feeding: On current year foliage

*Forced feeding: On older foliage.

Forced feeding simulated the situation following release phase when
mostly low quality needles would be available. The low nutrient
quality and probably relative quantity in the older foliage was
indicated by high frass production. Exhaustion of food may be suicidal
when dispersal is not possible. Exhaustion of high quality food
reduces survival rates (see also Mason and Thompson, 1971), and
probably quality which may be reflected in fecundity. Food quantity
affects size of adults, thereby their fecundity.

Leonard (1970) advanced a provocative hypothesis on several
aspects of population regulation in the liparid, *Lymantria dispar*. He
reasonably suggested that starvation enhances dispersal. But to state

that "at high density dispersal is induced prior to the crush of the
population" is misleading because it implies dispersal is "induced"
socially or otherwise from within the population. Yet it is clear that
environmental forces are necessary for dispersal. He also suggested
that during evolution, loss of wings in the ♀♀ was accompanied by
population flushes or wide fluctuations. The flushes appear self
destructive, but because starvation enhances dispersal, they are a
mechanism which ensures gene flow and maintenance of variability in
the populations. At high density dispersal is induced before the
population crashes and this sows the seeds for new populations. This
erroneously implies that whenever we detect a population crash, the
insects have actually gone elsewhere. Whether or not loss of wings in
Douglas-fir tussock moth ♀♀ was compensated for by development of
dispersal mechanisms in larvae, the loss has not been very costly as
gene flow and mating are facilitated by the ♀♀ being almost stationary
and producing a sex pheromone, and the hairy nature of the larvae for
aerial dispersal.

Several biotic agents have been recorded with increasing
frequency in the field during the decline phase. Most of them have
been identified from rearing projects. Apparently, the most important
agent is a nuclear polyhearal virus (NPV). In Forest Insect and
Disease Survey Annual Reports, a condition was described in 1939 as a
wilt disease; in 1945 as a virus; in 1954 as a polyhedral virus, and
in 1955 as NPV. In 1952, a biological control attempt with a virus -
probably NPV - was undertaken against the tussock moth in B.C. NPV
has also been implicated in decline of several outbreaks in the U.S.A.

Through a life table - factor analysis approach, Mason and Thompson
(1971) found for a virus $d_x F$ of 41 percent. Hughes and Addison (1970)
have identified two strains of NPV in the tussock moth. The virus
prevents oviposition by ♀ tussock moths (Dahlsten, et al., 1970): it
is not clear whether this is due to effects on oöcyte development,
hormonal control of sexual development and activity, or behaviour.
Martignoni et al. (1969) found a cytoplasmic polyhedral virus in
Douglas fir tussock moths.

Where NPV has been claimed to cause significant mortality,
it has often done so after severe damage has already been inflicted
by the tussock moth. The virus appears to let the insect get out of
hand. Long lags are probably characteristic between populations of
these two organisms. Stress may be necessary before the pest succumbs
to the virus. Is stress provided by food shortages, and increase in
pest density? Is high density required as a sufficient means of
disease transmission in the population? Notwithstanding our lack of
understanding of such points, NPV is registered now in the U.S.A. for
use against the Douglas-fir tussock moth.

Circumstancial evidence indicates a red ant, *Formica
intergroides*, protects trees from defoliation by the tussock moth.
Active ant colonies (Figure 42) were encountered in the study area.
Their scarcity and uneven distribution in affected stands were apparent.
Macroclimatic factors related to aspect and elevation, and microsite
factors related to stand structure may limit establishment of colonies
in the study area. Hughes (1975) showed such environmental factors to
be limiting for colonies of two insect predators, *Formica rufa* and

Figure 42. Active ant colonies.

Top: Cherry Creek - 1975; colony behind the range pole.

Bottom: Mountain View; colony behind the log piece.
        Note some defoliation in adjacent trees.

F. lugubris in Wales.

Formica intergroides appears to displace forcefully tussock moth larvae from branches.[7] In the Coniferous Biome of North America some of the largest groups of birds feed on leaf eating insects. Orioles, Vireos are common in the interior of British Columbia, but their predatory influence may be insignificant in reducing insect numbers. Turček (1948) in Checkslovakia noted that toxic gypsy moth larvae are eaten by birds including orioles and starlings. In Germany, hole nesting and other birds also eat gypsy moths (Luhl and Watzek, 1976). So the presence of a toxin in Douglas-fir tussock moth larvae may make them poor, but not unlikely candidate for birds' food.

Cost of an outbreak

A decision to protect or to not protect forest resources has primary and external benefits as well as costs. Externalities are an important characteristic of the forest resource and decisions governing its management. Traditionally, managers measure quantitatively these benefits and costs, commonly in monetary terms. In a managed forest, direct costs of an outbreak are real as they represent assaults on capital investments made in it. In a natural forest, on the other hand, losses are real only to the extent that we recognize the current market value of the crop, and the cost of time during which the crop occupies the land. Time is not a free resource: this concept is acknowledged in all investment decisions in part by the use of discount rates. This

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[7] Observation by Dr. R.F. Shepherd, personal communication.

is true also for conventional cash flow stand analyses. Clearly, value
losses are sustained whether damage is done to natural or man-made
stands. Investments to reduce these losses are essentially not
different from any other in forest management. Because forest protection
must compete with other cultural treatments for scarce funds, there is
need to express costs and benefits in terms of a common parameter. This
is necessary also for analysing feasibility of, and ranking investment
projects to decide between alternatives.

How do we actually measure losses and benefits in an outbreak?
We face two basic problems here: (i) identifying sources of benefits and
costs, especially external ones, and (ii) quantifying them. The
sources may be more complex than was indicated by Stark (1975).
Difficulties involved in quantifying benefits and costs, especially
external ones such as soil protection and aesthetics, were evident at
the 1974, 25th Annual Western Forest Insect Work Conference, at Salt
Lake City, Utah, in discussions by several resource economists (Curtis,
1974; Michalson, 1974; Rivas, 1974; R.G. Williams, 1974). These
difficulties are real; yet there is undeniable need for undertaking
economic analyses to ensure maximum returns from investments. Economic
analyses of specific insect problems are scarce in the literature. As
we are unable to quantify convincingly many costs and benefits, the
best we can do is use classical criteria of Benefit-Cost ratio,
Internal Rate of Return, Net Present Value only as guides in the
investment decision. Many forest protection decisions are made on a
"gut feeling", or for political, strategic or speculated reason such
as the argument that fire hazard is a problem in defoliated stands.

In B.C., the public, as the major owner of the forest
resource, bears most of these losses. But some segments of society
sustain higher immediate losses than others. The cost of an outbreak to
a forest worker represents reduction in income as a result of depletion
of the resource following defoliation. The cost of an outbreak to
different workers may vary because of in situ differences in their
income. The more income one foregoes the higher the cost. For an
individual who becomes ill from conjuctivitus, dermatitis, pulmonary
and other ailments caused by toxins from the base of tussock moth's
urticating hairs (Gilmer, 1923; U.S.D.A., 1973b; personal observation[8]),
his costs may be significantly higher. The cost to a grazier may even
be offset by increased forage following defoliation. Consider loss of
a Christmas tree crop at Pritchard, B.C. (FIDS, 1948), and of
shelterbelts around farms and residences in Idaho and Washington
(Tunnock, 1973): the tree farmers and residents did not sustain equal
losses. For a forestry enterprise which is dependent on backward
integration of the resource for survival and competitive ability, an
outbreak is a matter of life or death. These differences in sustained
costs stem mainly from the externality characteristic of the resource,
and its specific ownership pattern.

In landscape architecture and urban forestry, quantifying
value of a damaged tree is equally controversial. The value may be
equated with the amount of money an owner is prepared to pay in order
to save the tree. But various owners would spend different amounts of

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[8] I witnessed a faller complain of serious skin irritation while
logging a devastated stand owned by a Mr. Inskip, at Mountain View.
This was in the stand shown in figure 40 - bottom.

money for the same tree. It is generally agreed that one of the follow-
ing is the real loss to insect kill: (i) the current market value of
the tree regardless of historical costs; or (ii) the cost of establish-
ing a new tree up to the age, size and value of the dead one immediately
prior to its destruction. These concepts are often used in forest
property compensation. Aesthetic values of trees in the wilderness
are even more difficult to quantify. The value of trees in a park
may be assessed by visitor use. But what is the value of trees along a
public highway? Evaluation of values here becomes a problem of
evaluating mainly social attitudes.

Wickman and Renton (1975) explored two simple methods of
evaluating cost of one outbreak in a Pine-Fir campground with 8 units,
in California.

(i)   Following tree mortality, cleaning up was required to
      reduce fire hazard, and danger to camp users. Felling of
      dead and dying trees, and slash disposal cost $90.00.
      Topping top killed trees cost $100.00. The total cost was
      $190.00 ($23.75 per unit).

(ii) There were 370 trees in the campground, or 46.2 trees per
      unit. The replacement value of each unit was given as
      $1500.00. Assuming the Pine and Fir trees have equal
      aesthetic appeal, the value of each tree equals $33.00. A
      total of 25 trees were killed by the tussock moth outright:
      total value lost in mortality equals $825.00. To this
      should be added the cost of tree felling and topping ($190.00)
      from (i). Total loss amounts to $1015.00 ($126.00 per unit).

The first procedure is unacceptable as it ignores replacement costs. Both procedures unrealistically ignore possible reduction in visitor use related to lower aesthetic value, and annoyance caused by the tussock moth. I submit that the real cost of an outbreak is heavily dependent on "whose horse is getting gored".

Recently a new concept called Allowable Cut Effect, dubbed ACE, has appeared in the forestry literature (Schweitzer et al., 1972). The concept is not subscribed to unanimously. The concept: in a regulated forest with some old growth where yields are constrained artificially and regulated, any silvicultural treatment which increases yield in second growth should justify our reaping benefits of increased yield immediately in the old growth. The immediacy of these benefits results in highly favorable Internal Rates of Return. ACE is real, and is demonstrable in conventional stand analyses. The fact that it can be traced to in situ artificial constraint on the yield does not nullify its reality.

Strictly on the basis of conventional investment cash flow analysis applied to protection of forest inventory, Bell et al. (1975) implied that we often exaggerate the cost of an outbreak. While ACE is used to promote some stand improvement investments, it can be used to discourage others such as protection of inventory: "...like the two edged sword, ACE can cut in both directions." Bell et al. (1975) used data from a case study of the latest tussock moth outbreak in the Umatilla National Forest. The U.S. Forest Service had estimated the damage there to be over two million dollars. But Bell and his associates argued as follows:- In that outbreak, nonsalvageable mortality

amounted to about 1.2 million board feet (fbm) every year for the next

rotation of 115 years, or 1.2 million fbm of the allowable annual cut

in the management unit. The loss was calculated according to the

familiar Hanzlik formula, which is now obsolete in that area. At the

market value of $62.00 per thousand fbm, the loss was $74,400.00

annually. In cash flow investment theory, this represents a series of

annual payments for a terminable period of 115 years. Assuming a

reasonable discount rate of 10 percent, and using the appropriate

investment model[9] to discount to the present, the loss amounted to only

$744,000 (cf. more than $2,000,000.00).

The undiscounted loss is so high because the cost is borne

only by the present generation. It is equivalent to using zero

discount rate. As in depreciation theory, these costs should be

spread over a meaningful period - a crop rotation in this case. Insect

damage may not result in as much losses as we often think. Because of

higher timber values and shorter rotations on better sites, discounted

losses are likely to be higher there. Such sites deserve higher

priority in protection. Losses on poorer sites may be very low;

benefits accruing from increased forage production following defoliation

make the losses even smaller. This is an argument for leaving outbreaks

on poorer sites to run their course. If we invest money on such sites,

the opportunity cost we incur may be too high. The younger the stand

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[9] $V_o = r/i \left[\dfrac{(1+i)^n - 1}{1+i)^n} \right]$ where V_o = discounted value; r = annual payment; i = discount rate; 10% = 0.1; n = number of years - rotation.

Bell et al. did not give their model. Results obtained from this one were slightly different from theirs. Reduction of the discounted loss is indisputable!

when it is damaged, the less value we lose through mortality. For

various reasons, discount rates lower than 10 percent are more realistic.

But to exclude discounting at all is unacceptable. When outbreaks are

recurrent, as they are within some management units, loses may overlap

and magnify over a single rotation. Because values of stands differ by

location and other characteristics, and because discount rates also

differ in time, we obviously need detailed evaluation of benefits and

costs for each specific problem in order to determine its real magnitude

before attempting serious control measures. A blanket control project

in the study area is unjustified. It may also be undesirable when we

examine benefits accruing to forage production if an outbreak is left

alone on some sites.

> "... involvement in resource protection from insects
> and diseases has been oriented toward protecting commercial
> timber values. Where these values are low ... but where
> watershed, wildlife, esthetics and recreational values
> of a vigorous forest are high, we need to rethink our
> priorities." John R. McGuire, Chief, U.S. Forest Service,
> 1976.

Resource use conflicts and pest management strategy

It is unwise to advocate pest management strategies without

considering the land or resource use pattern in an outbreak area. Mere

visual impacts on trees should not necessarily lead to invoking of pest

suppressive measures. Sometimes for various reasons it is more

sensible to leave an outbreak alone unless it threatens valuable stands.

Where several resources are involved on the same land, as in the B.C.

interior, it is important that we consider all resources, not only one.

It may be easier to decide on the strategy when the sympatric resources are compatible. In this section I will consider two apparently "conflicting" resources in the study area - forage and tree production - in developing a strategy for managing the Douglas-fir tussock moth. In my arguments, I will rely heavily on the data and foundation established in preceding sections.

Inasmuch as land tenure is indicative of land use priorities, when protection of forest inventory is considered it is imperative that we consider the resource values and their relative importance in the whole. The relevance of forest land tenure - the interphase between forest law and economics - in forest resource use is apparent, especially in expanding scope of forest resource management. On the Canadian scene, most forest land tenures such as those in the public domain are indicative of relative magnitudes of resource values on the respective land.

Within the Interior Douglas-fir Zone about 3.2 million forested hectares were being used for grazing twenty years ago. This included all the lower zonal ecotones. In contrast, there were 1.2 million hectares of open range most of them below the timber line (Sloan, 1956; Tisdale and McLean, 1957). More recently Pearse (1976) put the total area of usable forested range land at about 6.7 million hectares, most of which are in the Kamloops and Cariboo Forest Districts. Evidently, the interior forests are important sources of forage. In the open range, forage production is the dominant, and often the only tenured use. Tenure on forest land is variable. The study area is surrounded by several Public Sustained Yield Units (PSYU) and Tree Farm

Licences (TFL). All of my study plots were within the Kamloops PSYU
(No. 31). Within the unit, some land is privately owned.

P.S.Y.U.'s and T.F.L.'s are dominant at higher elevation,
where wood and fibre production are primary uses, and forage rights are
usually for one year in the form of grazing permits. In the ecotone,
many stands are managed under 21 year grazing leases; here forage
production is dominant over timber production. But logging may be
undertaken in emergency to salvage timber values through Timber Sale
contracts while the lease is still valid. The forested land covered by
these leases is administered under the Land Act, and is of low site
quality for timber production. Many of the defoliated stands were on
such land (Table 2). The low site quality is evident also in low
timber yields extracted during logging. On most of the privately owned
forest land, grazing is the dominant, but not necessarily the only use.

Inasmuch as the public makes various overlapping demands
on the ecosystem, conflicts in resource use and management are bound
to arise. One of the most serious and oldest conflicts here involves
range and timber values. Professional resource managers, graziers and
others have been involved in the conflict. As early as 1920 the pro-
vincial minister responsible for forest resources, the Hon. T.D. Pattullo,
stated that of the forested land 3.8 hectares were potentially suitable
for agriculture and would be put to farming (probably forage production)
after timber harvesting. The withdrawal seems not to have materialized
to a significant extent as there were 3.5 million hectares of forested
range land thirty-six years later (Sloan, 1956). In his Royal
Commission reports, Chief Justice Sloan (1945, 1956) considered the

issue of multiple use, especially in the interior, as one of the most

controversial in management of the provincial forest resource. It

was during the 1955-1957 commission hearings that the controversy

between range and timber interests reached its apogee.

> "It is chiefly in relation to grazing on crown forest
> land that conflicts of interest arise. (The use of)
> the land for production of timber, cattle, the
> extraction of minerals and available water ... will create
> ... unfortunate, although presently avoidable
> consequences". (Sloan, 1956; p. 681).

It is fallacious to believe that resource conflicts are due solely to

mismanagement, contrary to the Argument of Crown Counsel, section 199

(Anon. 1956):

> "One witness said pithly that there was room for both
> loggers and cattlement if the matter is properly
> managed."

In a brief, a Mr. T.G. Willis, an agrologist with the then Dominion

Agriculture:

> "Their (graziers') other problem is the encroachment
> of the forest on their grazing land. Stockmen have
> been agitating this matter for a number of years, so far
> without any tangible results."

"Jack (Lodgepole) pine, willow and alder" are blamed for the forest

encroachment. In concurring with these opinions, Sloan called these

trees trespassers, and erroneously considered the encroachment problem

more serious than overgrazing. The same attitude had been set in his

earlier report (Sloan, 1945; p. 164). But as forester Alan Moss

testified:

> "We (the interior forest industry) are just as touchy
> about encroachment of (sic) forest land by grazing
> land as the cattle industry is on the encroachment
> of grazing land by forestry" (Sloan, 1956; p. 699).

In view of the broad frame of reference for the commission, it is surprising that equally important questions of forage yields and quality, timber yields and soil conservation influences by ecological forces (e.g. insects) other than logging appear to have largely been ignored.

The broadening scope of forest resource management necessitates that the basic objective of pest control measures be one of minimising damage or losses not necessarily to one, but several resources in the ecosystem. Because control measures have beneficial and detrimental externalities, we need to think in terms of the whole system. The resources considered are probably variable in space and time, and they are not of equal importance. Any attempt to evaluate impacts in a forest ecosystem necessarily involves investigating parameters closely associated with the resources of interest. The pest management strategy should take into account, among other things, the extent of and variation in the resources and impacts of the damage.

On poor and low sites, control of the Douglas-fir tussock moth would be justified if the objective was to decimate populations from potential epicenters. But contagious spread in this insect is insignificant (Mason and Thompson, 1971; Mason, 1974; Wickman et al., 1973). If (passive) contagious spread was significant, it would likely be for long distances. Presence of the insect in major valleys in the area, where cross valley and north$\longleftrightarrow$south winds are common suggests some populations are probably related, but in a way which is difficult to predict from dispersal patterns. So far the evidence indicates that patches so common on the landscape represent different native or autochthonus populations. Controlling the foci is sound only to the

extent that it prevents damage of resources within the infestation patch. The "nip-in-the-bud" concept (Stehr, 1968) is not relevant beyond the patch because decimating the insects in one patch does not affect those in another. The three year cycle may describe adequately individual populations, but in the field often populations are not in phase with each other. On the landscape longer cycles are not uncommon. A broadcast control treatment is inefficient unless it is applied only on the good and medium sites and when most populations are in the same vulnerable phase, before eruption or crisis. As populations are "independent" and infestations last for a few years, control is likely to be spread over as many years. Some stands may have to be treated more than once.

High rates of tree mortality are probably due to chronic infestations. It should not be assumed that every tree which has been stripped of its foliage will die. It is unrealistic to invoke control measures in a stand during the first year of infestation on grounds that we are preventing trees from dying. Most outbreaks in the past collapsed naturally, although often after severe damage had already been inflicted. Most control attempts were undertaken during the outbreak phase. Since most populations are not in phase with each other, claims of successful control from a single broadcast treatment may be suspect. Likely the populations would have collapsed naturally, as they have many times in the past. Any spurious claim of successful control is dangerous from at least two angles: it justifies expenditures unwisely spent, and sets a precedent on which future control attempts will be based on the premise that "it worked the last time".

A decision which advocates no control in some areas requires less cash outlay. It also realizes benefits in forage yields. On south and east facing slopes providing winter refuge for mule deer, the decision assumes special dimension. High increases in forage yields should be expected on mesic sites with deep sandy loam soils. Such sites may produce high timber values but control should not necessarily be the rule there, especially when the stands are managed primarily for forage, or wildlife refuge.

Conclusion

By reducing stand stocking and density, the Douglas-fir tussock moth increases range forage production. Significant gains should be expected on mesic sites, in more intensively chronically infested stands, and in dead patches of trees. Salvaging infested stands increases the benefits, especially when followed by range seeding.

Tree survival is affected by defoliation, and is related to size and possibly other factors. Effects on tree radial growth at breast height are not significant during the first year following defoliation. I did not investigate effects beyond the first year.

It is true that various degrees of contagious spread of tussock moth populations by wind dispersal of the larvae are inevitable. Nevertheless the strong possibility remains that existing widespread populations have their own independent capability of erupting under the blanket conditions of weather systems which favor population

increase generally. Delayed eruptions in some localities do not necessarily signify that they originated from "hot spots", but may signify that the microsite conditions were somewhat less favorable, and thus created a lag.

Advocating a broadcast control of the pest is unwise because it leads to spending money on low quality sites and on sites which are managed primarily for forage production. It also prevents realization of range benefits. Suppression measures may not prevent remote stands from being infested because contagious spread is not common. Selective control, with better sites given priority, will improve efficiency of investing scarce funds.

There is need for undertaking similar studies in other affected localities to obtain data from a wider base more representative of the Interior Douglas-fir Dry Subzone. Because outbreaks are recurrent, it is relevant to study impacts in a long term mission oriented research. But we need to know the specific history of stands, and possibly individual trees, if we are to state long term impacts confidently. There is also need to examine changes in forage yield and quality at the species level to provide most meaningful data to range and wildlife managers and graziers. Possible confounding of yield data may be avoided by using exclosures.

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Appendix

SCIENTIFIC NAMES OF PLANTS

Trees

|	
Balsam fir	*Abies balsamea* (L.) Mill.
Black cottonwood	*Populus trichocarpa* Torr. & Gray
Black spruce	*Picea mariana* (Mill.) BSP
Black tupelo	*Nyssa sylvatica* Marsh.
Choke Cherry	*Prunus virginiana* var. *melanocarpa* (A. Nels.) Sarg.
Douglas-fir (interior)	*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*
Douglas maple	*Acer globurum* Torr. var. *douglasii* (Hook) Dipp.
Engelmann spruce	*Picea engelmannii* Parry
Grand fir	*Abies grandis* (Dougl.) Lindl.
Jeffrey pine	*Pinus jeffreyi* Grev. & Balf.
Longleaf pine	*Pinus palustris* Mill.
Ponderosa pine	*Pinus ponderosa* Laws.
Subalpine fir	*Abies lasiocarpa* (Hook) Nutt.
Western hemlock	*Tsuga heterophylla* (Raf.) Sarg.
Western larch	*Larix occidentalis* Nutt.
White fir	*Abies concolor* Gord. & Glend.

Understory vegetation

Balsam root	*Balsamrhiza sagitata* Nutt.
Blue bunch wheat-grass	*Agropyron spicatum* (Pursh) Scribn. & Smith.
Downy brome	*Bromus tectorium* L.
June grass	*Koeleria cristata* (L.) Pers.

Kentuky bluegrass   *Poa pratensis* L.

Needle-and-thread   *Stypa comata* Trin. & Rupr.

Pine grass   *Calamagrostis rubescens* Buckl.

Sagebrush   *Artemesia tridentata* Nutt.

Timber milk-vetch   *Astragalus miser* Dougl. ex Hook

FIGURE 3. Extent of the outbreak in the study area in 1976.

Sample plot localities

1 Cherry Creek
2 Indian Gardens
3 Mountain View
4 Dairy Creek
5 Heffley Creek

KAMLOOPS LAKE

BRITISH COLUMBIA

KAMLOOPS DIVISION OF YALE LAND DISTRICT

Scale 1:125,000 or approximately 2 Miles to 1 Inch.

Scale of Kilometres

Magnetic Declination approximately 23°10' East at centre of map, 1968.
Decreasing approximately 3'10" annually.

Universal Transverse Mercator Projection

Maps and indexes with price lists may be obtained
from the Map Production Division, British Columbia
Lands Service, Parliament Buildings, Victoria, B.C.

REFERENCE

RELIABILITY

Planimetry compiled from B.C. Prov. Govt. air surveys interim
mapping, 1950, and 1954. B.C. air photos 1948, 1950, and 1952.

Contours compiled from mapping by Dept. of Energy, Mines and
Resources, Ottawa, 1952.

Culture revised from B.C. Prov. Govt. air photos 1966.

KAMLOOPS LAKE, B. C.
SHEET 92 I/NE
SECOND STATUS EDITION