# NET PRIMARY PRODUCTIVITY AND PEAT ACCUMULATION IN SOUTHEASTERN MANITOBA

A Thesis

Submitted to

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in Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

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I often say that when you can measure
what you are speaking about and express
it in numbers you know something about it.
But when you cannot measure it, when you
cannot express it in numbers, your knowledge
is of a meager and unsatisfactory kind.
It may be the beginning of knowledge,
but you have scarcely in your thoughts
advanced to the stage of science.

Lord Kelvin

dedicated to May 6, 1967

ACKNOWLEDGEMENTS

The information presented in the following pages has been accumulated with the help of a number of interested individuals.

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ABSTRACT

Two functional attributes of an ecosystem, net primary production and subsequent dry matter accumulation, were examined in four peatland types (lagg, bog, muskeg, and bog forest) located in southeastern Manitoba.

The simple equation "accumulation = income - loss" was expanded in a block diagram to define all potential sources of both income and loss. Annual "income" of litter in the four vegetation zones ranged from 489 to 1750 gm./m.$^2$, which represented 69-90% of the calculated net primary production. "Loss" of dry matter through decomposition in the following year amounted to approximately one quarter of the litter value. Using radiocarbon-dated peat cores, an average annual accumulation rate of 26-51 gm./m.$^2$/yr. was calculated, suggesting that less than ten percent of the annual net primary production will remain as peat.

The four vegetation types examined were considered to represent seral stages in the process of secondary succession occurring in the study area. The direction of this succession was hypothesized to be Lagg -> Bog -> Muskeg -> Bog Forest.

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# Chapter I

## INTRODUCTION

A. Statement of the problem

Man is dependent on the photosynthetic process for personal energy, as well as for the accumulated organic reserves which power his industrial society. In view of today's expanding population and environmental pollution it has been stressed that scientific management of world vegetation is essential. However, to utilize this natural resource efficiently the production potential of various vegetation types must first be established.

Not only are production studies economically important, but they also aid the ecologist in his quest to better understand the ecosystem. Gates (1968, p. 5) considered production studies to be one of the five most important considerations made in studying natural systems. Whittaker (1961, p. 179) went one step further when he stated that production seemed to be the best single dimension by which species could be ranked according to functional significance in the ecosystem.

A peatland[1] is one ecosystem in which little is known about the productivity of vegetation present. Knowledge of this production is then most desirable, especially in Canada, which has an estimated $I.I \times 10^8$ hectares of peatland (Burke & O'Hare, 1962, p. 647). Added impetus for the study of production in the

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[1] See glossary (Appendix C)

peatland ecosystem comes from the fact that peat represents a natural product. It is important not only as an economic resource, e.g., fuel, agriculture, soil additive, poultry litter, peat wax, etc. (Bellamy, 1966, p. 15), but also in maintaining a balanced environment, where it serves as a reservoir for large quantities of both carbon dioxide and water (Deevey, 1958, p. 120). Therefore, the following two questions were posed for further consideration:

(1) What is the productivity of peatland vegetation at a site in southeastern Manitoba?

(2) What is the annual accumulation rate of peat in relation to the amount of this production?

B. Literature review of the concepts of production and accumulation

Thienemann (1931), cited in MacFadyen (1948, p. 77), and Engelmann (1968, p. 74) both mentioned that the term "production", as used by the ecologist, had a connotation not usually expressed in a standard dictionary. It is the ecologist's interest in community energy and dry matter flow that has led to the terms "production" and "productivity" being given special technical meaning (MacFadyen, 1948, p. 75).

Most definitions of production are based on the concept implied in the following generalized photosynthetic equation:

$$6\ CO_2 + 12\ H_2O \xrightarrow[\text{chlorophyll or other pigment}]{\text{673 kilocalories}} C_6\ H_{12}\ O_6 + 6\ O_2 + 6\ H_2O$$

The formation or production of organic compounds by plants directly from solar energy and inorganic raw materials is referred to as primary production. Previous authors have defined the rate of production, i.e., productivity, in terms of either the organic matter produced (Blackman, 1968, p. 243; Ovington, 1965, p. 296), the chemical energy which this organic matter contains (Odum, 1959, p. 68; Scott and Billings, 1964, p. 265; Woodwell and Whittaker, 1968, p. 19), or the organic matter and energy produced used as equivalents (Westlake, 1963, p. 388).

If the amount of synthesized organic material available for harvest by man and other animals is considered, two defini-

tions for primary productivity are necessary:

> ...Gross productivity is the rate of production of new organic matter, or fixation of energy, including that subsequently used by the plant and lost as heat; that is, the observed change in biomass plus all losses, including respiration divided by the time interval. (Westlake, 1966, p. 317)

> ...Net productivity is the rate of accumulation of new organic matter, or stored energy; that is, the observed change in biomass plus all losses except respiration, divided by the time interval. The net production is the organic material or energy available for exploitation by secondary producers or consumers. (Westlake, 1966, p. 317)

Odum (1959, p. 68) and Milner and Elfyn Hughes (1968, p. 4) have equated the above concept of net productivity to the terms "apparent photosynthesis" (Pearson, 1965, p. 278) and "net assimilation". Davis (1963, 1967) however, observed the need for a further distinction in the definition of net primary production. He considered there to be "...no constant proportionality between net primary production of organic matter and the net primary storage of energy" (Davis, 1967, p. 253). It is possible that equal weights of newly synthesized organic matter would have different energy values, since this value depends on relative amount of lipid, carbohydrate, and protein synthesized. Therefore, he referred to the net rate of synthesis of organic matter as "net primary organoproductivity", while "net primary energoproductivity" referred to the net rate of formation and storage of potential chemical energy. Only "net primary organoproduction"

was determined in the current study. This has the following components:

net primary organoproduction per growing season = weight of new aerial and subsurface vegetation components produced in the current growing season

+

weight of organic matter produced in the current growing season but lost through death, leaching and exudates

+

weight of organic matter produced in the current growing season but lost through consumption

+

weight of material translocated from new to old growth as reserve

-

weight of reserve translocated from old into new growth

So far only the creation of organic material has been considered, i.e., the production process. With cell death, the organic compounds produced in the above process become fragmented into smaller compounds through the process of decomposition. Other losses occur through consumption by herbivores. If the rate and amount of initial net production exceeds the subsequent rate of consumption and decomposition, the result is a net accumulation of organic matter.

Ecologically, Olson (1964, p. 101) has defined accumulation as "income minus loss". With reference to the peatland ecosystem, the process of accumulation can be summarized as follows. Each growing season there is a net production of organic matter, some of which dies at the end of the same season. This material, including the contribution made by perennial portions, represents "income" in the accumulation process. Of this income a fraction is lost through decomposition in subsequent years. This relationship may be expressed by the following equation:

| | | | |
|---|---|---|---|
| accumulation = | income of litter resulting from net primary production | - | loss through decomposition |

The objective of the present study was to determine the magnitude of the components of this equation for a peatland in southeastern Manitoba.

C. Methods employed to calculate plant production and peat accumulation

A number of methods have been proposed for general use in studies of terrestrial primary production. These have been summarized by Odum (1959, 1968), Lieth (1965), and Woodwell and Whittaker (1968). Yet, in any specific investigation the replacement rate for plant parts must be considered before a method for the measurement of productivity can be decided upon. In cases where the turnover rate of plant parts is rapid, biomass fluctuates little over the growing season and measurement of biomass change with time does not indicate the true rate of production. However, in the peatland ecosystem the replacement of plant parts is minimal in a single growing season. Therefore, the observed change in plant biomass was used as the basis for the measurement of annual net primary production.

Odum (1960, p. 35) suggested that since the point of maximum biomass is reached at different times for various species, then changes in plant biomass should be calculated for a continuous series of short term intervals over the entire growing season. This "short-term harvest method" allows a better estimate of maximum net primary production to be made.

Total net primary production can be calculated either as the sum of individual species' biomass peaks, or can be based simply on the peak ecosystem biomass, without calculating indi-

vidual species' peaks. Malone (1968, p. 434) suggested that this latter approach was valid only when the dominant species had similar phenologies.

Most previous production studies have concentrated on a total quadrat approach. All plants are harvested from a number of representative areas, and in each species the mean weight increment per sampled area is equated with production. Yet, from one sampling date to the next, plant weights change not only because growth has occurred, but also because the number of individuals in the sampled areas is different (Traczyk and Traczyk, 1967, p. 833). Without determining the number of individuals harvested at each sampling date it is not valid to conclude that the observed weight change is due to growth alone. Therefore, in the present study net production was determined on an individual plant basis. Small representative areas of vegetation were harvested, and the number of individuals of each species present was counted. This allowed a density value to be calculated for each species. Mean annual production per individual was then determined for each species as indicated on pages 54 and 81 and estimates of production on an area basis were made for each species by multiplying mean production per individual by density (Traczyk, 1967, p. 839-842). The annual production total for the community was calculated as the sum of the individual species'

production values.

Although production must occur before accumulation of organic matter can take place in the peatland ecosystem, the rate of end product accumulation has received most attention in previous investigations. A variety of methods have been employed to estimate the annual peat increment, most involving direct measurement of the height or weight of existing peat reserves. Dividing height or weight values by the radio carbon age of the same portions provides an estimate of the annual accumulation rate of peat.

In the present study, the average annual accumulation rate of peat ($\Delta A_t$), was first calculated as:

$$\Delta A_t = \frac{\text{total measured weight or height of peat}}{\text{radiocarbon age of total weight or height}}$$

By determining values for both "income" and "loss" in the accumulation equation below, an annual surface accumulation rate was also calculated.

$$\Delta A_{1970\text{-}71} = A'_i = A_i - K'(A_i)$$

$A_i$ = income of litter from current net primary production and from perennial plant portions, including plant secretions ($Sc_p$); all sources measured during 1970

$\Delta A_{1970\text{-}71} = A'_i$ = amount of initial peat-forming material remaining at the end of 1971

$K'$ = decomposition rate of litter (1970-1971)

The value $A'_i$ represented the annual accumulation rate of surface material, since further decomposition would take place in the fraction remaining at the end of 1971.

Estimating the fraction of original litter which eventually remains requires an understanding of the decomposition process.

The mathematical function describing the course of decomposition in a peatland environment is linear,according to observed values of decomposition in fern petioles over a period of seven years (Frankland, 1966, p. 46). Gore and Olson (1967, p. 301) have assumed the fraction remaining to decrease exponentially with time. A subsequent investigation (Minderman, 1968, p. 360), has indicated that decomposition of individual chemical compounds may indeed be exponential in nature, yet the observed decomposition rate for the combination of these components is less than exponential. Minderman therefore concluded "...This makes it questionable whether a logarithmic function is better than a linear one for describing the course of decomposition."

In most terrestrial ecosystems it can be expected that the decomposition of annual litter will eventually proceed to completion, with all compounds broken down into constituent elements. However, in a peatland environment anaerobic conditions prevent complete decomposition, resulting in an accumulation of

inert peat (Waksman and Stevens, 1929, p. 315).

The degree of completion to which decomposition proceeded in the litter of surface vegetation was not measured in the current study. Hence, the value of $\Delta A_t$ was the only estimate available for the annual accumulation rate of peat. This $\Delta A_t$ value represented the average accumulation rate of the combination of peat types accumulated during the past, rather than for individual surface vegetation types now present.

The relationship between "income" and "accumulation" of surface vegetation was obtained from the value of net primary production and the amount of this production remaining after one year of decomposition ($A'_i$):

$$\text{surface accumulation ratio} = \frac{A'_i}{\text{total current net primary production}}$$

The derivation of current net primary production and surface accumulation values was carried out in two steps:

(1) Defining a peatland area where the processes of production and accumulation were taking place.

(2) Constructing a scheme to represent the process of net primary production and the subsequent accumulation of peat. This scheme formed a framework for the calculation of empirical values for both production and initial accumulation in the defined area.

# Chapter II

## DEFINITION OF A SITE FOR INVESTIGATION

A. Location

Based on a preliminary ground and air survey of peatlands located in southeastern Manitoba, an area in the Whitemouth Valley (Lovering, 1961, Figure 1) was selected for intensive study. Both its accessibility and the variety of vegetation patterns shown in a relatively small area (Figure 1d) made it suitable for comparative productivity studies.

The peatland is found mainly in Section 19, Township 10, Range 12 EPM, approximately 3.2 kilometers (2 miles) southwest of Elma, Manitoba (49° 53' N, 95° 54' W). This section represents a small extension of a larger peatland found directly south of the study area (Figure 1c). Access to the site is from a dirt road adjacent to the north side of the peatland.

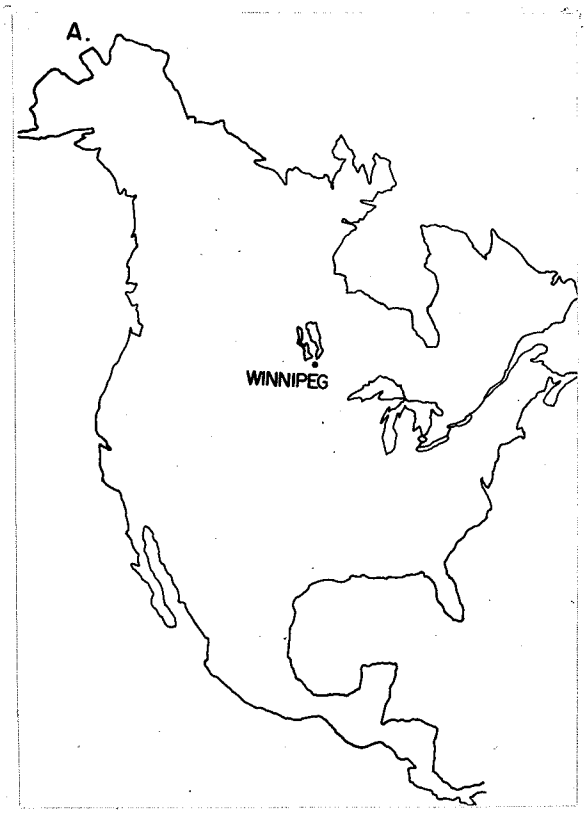
Figure 1. Location of the peatland studied.

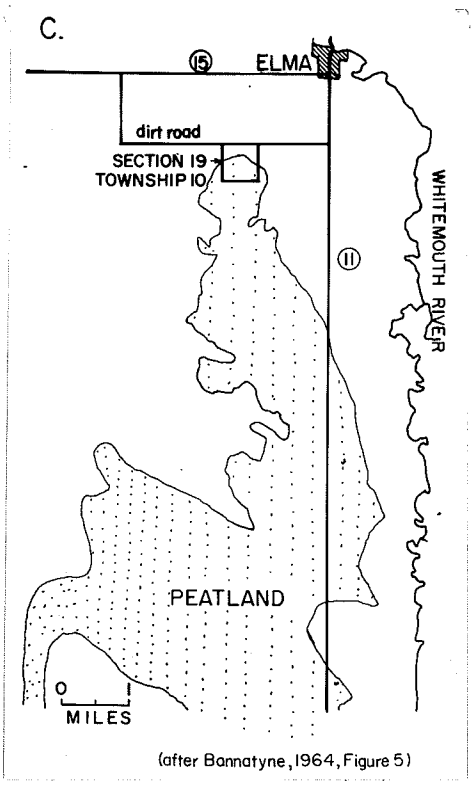
A. position of Winnipeg in relation to North America

B. position of Elma in relation to Winnipeg

C. position of Section 19 in relation to Elma

D. position of the study area in relation to Section 19

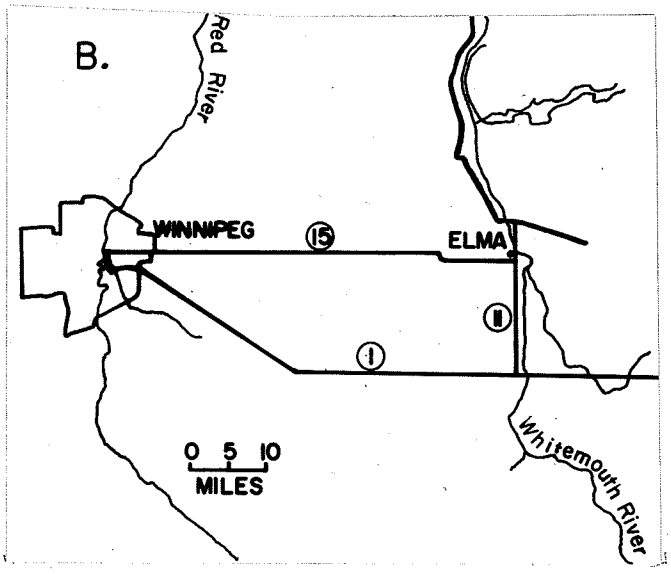

A.
WINNIPEG


C.
15
ELMA
dirt road
SECTION 19
TOWNSHIP 10
11
WHITEMOUTH RIVER
PEATLAND
0
MILES
(after Bannatyne, 1964, Figure 5)

N

W E

S


B.
Red River
WINNIPEG
15
ELMA
11
1
0 5 10
MILES
Whitemouth River


N

B. Environment

According to Gorham (1957, p. 152) "...the way in which peat accumulates varies almost infinitely in response to different combinations of environmental factors." He suggests that the observed peat accumulation in any specific situation is a result of the interaction of four major factors; namely, geology, topography, climate, and biotic influences.

I. Geology

While nearly all of the Whitemouth valley is underlain by Precambrian crystalline rocks (Lovering, 1961, p. 8) determination of the exact nature of the bedrock in the Elma area has been hampered by the thickness of the surface glacial drift (Davies et al, 1962, Figure 36). The influence of two glacial ice sheets and Lake Agassiz I and II in this region (Dachnowski, 1925, p. 348; Prest, 1965, p. 19) has been described by Smith et al (1967, p. 15) as follows:

> As the ice melted, the rock materials were deposited as glacial drifts in various forms. The drift deposits, along with small areas of recent alluvial deposits of the present streams, wind blown sand and organic deposits, constitute the parent material from which the soils have developed.

The peatland itself appears to be underlain totally by quartz silt, as determined by peat borings in the study area (Figure 6), and at a location in the interior portion of the

peatland by Bannatyne (1964, p. 17). However, the influence of this quartz silt on living vegetation will depend on the depth of peat between it and plant roots.

2. Topography

> The main ecological function of land form lies in determining local moisture conditions, as against the general pattern controlled by climate; but the nature of relief also has an important influence upon the flow of nutrients leached from the soil by rain (Gorham, 1957, p. 155).

The peatland under study occupies a slight depression in a region which is otherwise quite flat, Township 10 having a slope of 0-5 feet per mile (Lovering, 1961, p. 13). Nutrients from the surrounding mineral soils, which are of the grey wooded and rego humic gleysol type (Smith et al, 1967, Figure 8 and folder map), may indeed seep into peripheral portions of the peatland and make an important addition to the peatland's nutrient supply.

While there are no open water entrances, exits, or reservoirs found on the peatland itself, ground water may provide some of the moisture required by surface vegetation. Observations made during the study period indicated that ground water changes followed the annual pattern first described by Manson & Miller (1955), as cited by Heinselman (1961, p. 22), and later by Bay (1967, p. 35). The water table rose rapidly to the surface following spring snow melt, with a recession during the summer, when precipitation was insufficient to compensate for evapotranspiration,

and continued low levels through the winter. From the time of snow melt in April, 1970, the water table remained level with surface vegetation until the end of May, 1970. By the middle of August it had fallen 50 cm. below the surface. Subsequent rainfall in September brought the water level to within 20 cm. of the surface, where it remained during winter months.

3. Climate

Another source of moisture for peatland vegetation is atmospheric precipitation. Smith et al (1967, p. 20) have described the Elma area as "subhumid", with a definite summer maximum of precipitation: "Approximately 70% of precipitation falls as rain during the period of April to October and about 30% as snow during the five winter months of November to March." Monthly precipitation data was obtained from the meteorological station at Pinawa, Manitoba, 29 kilometers (18 miles) north of the Elma site. As indicated in Figure 2, a greater than average amount of precipitation fell during the 1970 growing season.

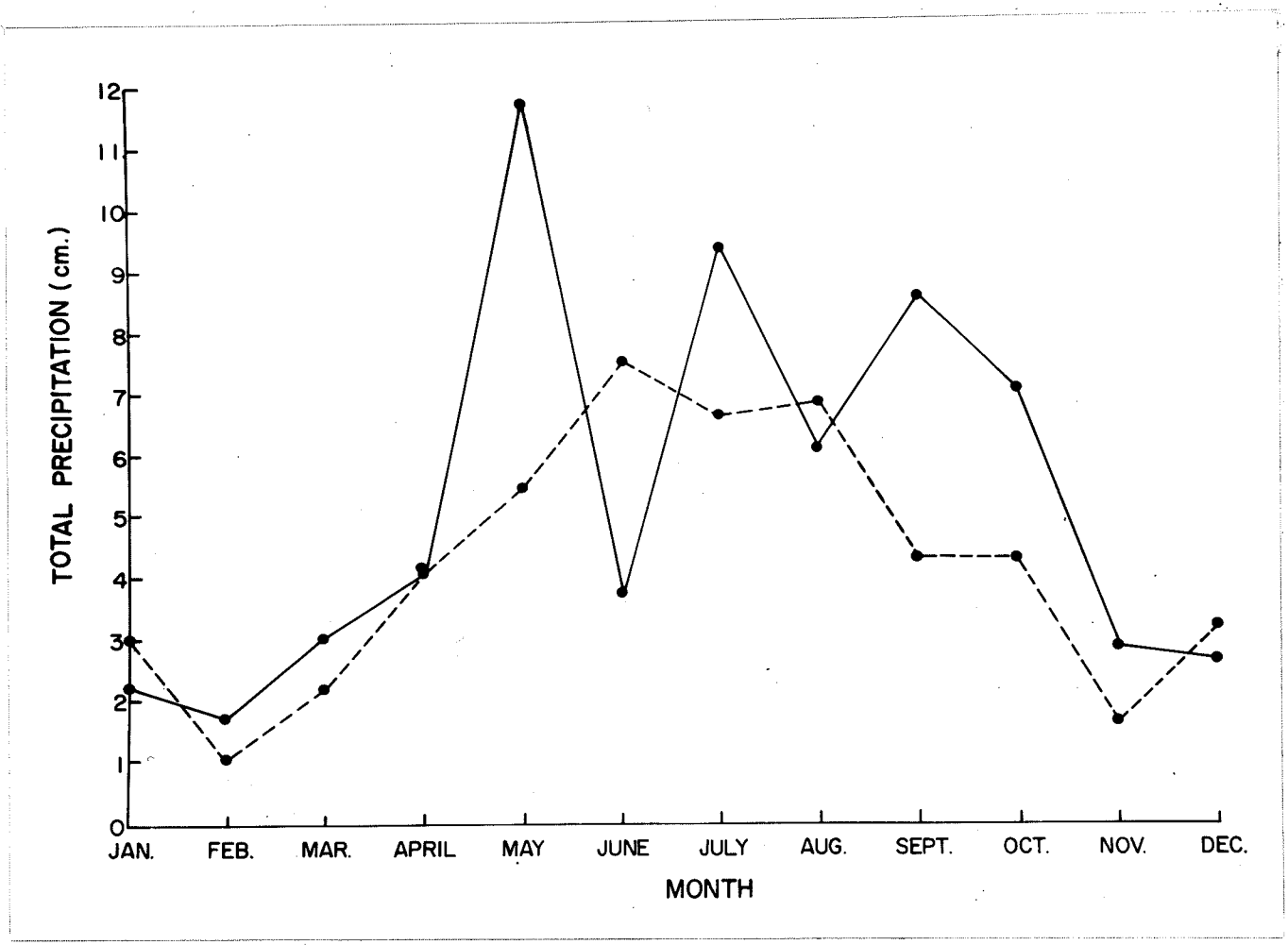
This atmospheric precipitation makes a major contribution to the nutrient budget of a peatland (Gore, 1968, p. 490). It also aids in the recycling of nutrients by leaching mineral elements from vegetation surfaces (Tamm, 1951, p. 184).

A description of the temperature conditions has been given by Smith et al (1967, p. 20):

Figure 2: Total monthly precipitation recorded at the meteorological station, Pinawa, Manitoba.

(i) monthly averages over the last four years (1966-1969)

(ii) monthly values in 1970


TOTAL PRECIPITATION (cm.)
0
1
2
3
4
5
6
7
8
9
10
11
12
JAN.
FEB.
MAR.
APRIL
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
MONTH

> This is an area which lies in the centre of the continent, a great distance from the oceans and their moderating effect on temperature. Summer temperatures are higher, winter temperatures are lower and the annual temperature range much greater than the world average for the latitude. ...temperatures are particularly variable during the spring, fall, and winter seasons, when the area is affected by frequent frontal disturbances between the cold "Continental Polar" air from the north and warm dry "Marine Polar" from the south. ...transition from winter to summer is abrupt, occurring normally in April, and the change from summer to winter is usually in October.

The temperature data obtained from the meteorological station at Pinawa, Manitoba was considered to be representative of conditions at Elma.

Mean monthly temperatures in 1970 were similar to the average of the previous four years (Figure 3).

Smith et al (1967) cite a figure of 111-127 days as an average length for the annual "frost-free" growing season, while during 1970 the growing season was 132 days, i.e., May 5 - September 14.

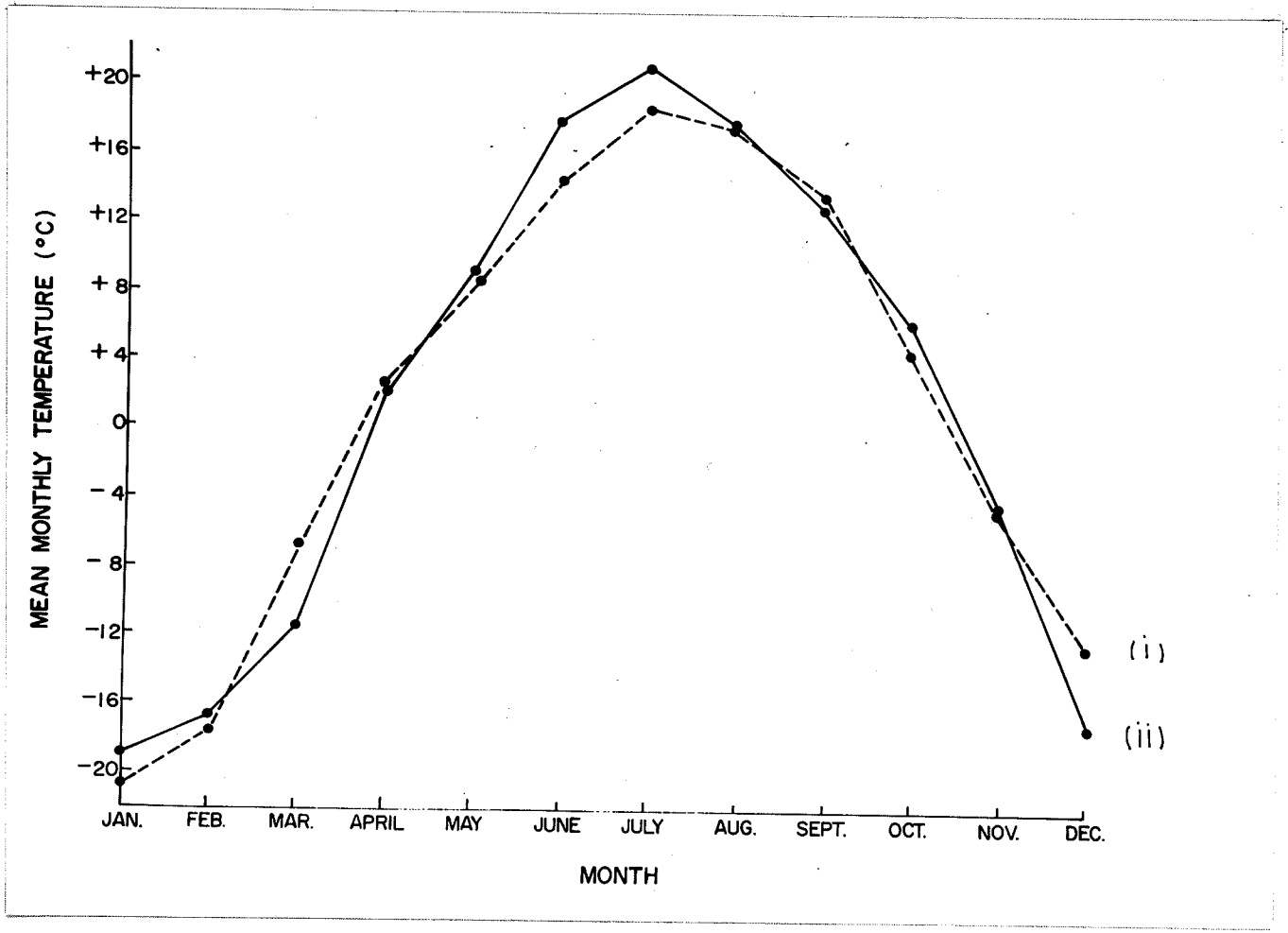
Unfortunately the conditions of climate to which young growing plants are exposed cannot be deduced directly from figures for climate published by nearby meteorological stations. This is due to the fact that meteorological elements are influenced by the nearness of the ground, and hence are subject to vertical change (Geiger, 1965, p. 2).

The existence of micro-environments in peatlands has been

Figure 3. Mean monthly temperature recorded at Pinawa, Manitoba.

(i) monthly averages over the last four years (1966-1969)

(ii) monthly values in 1970


MEAN MONTHLY TEMPERATURE (°C)
+20
+16
+12
+8
+4
0
−4
−8
−12
−16
−20
JAN.
FEB.
MAR.
APRIL
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
MONTH
(i)
(ii)

documented by Tsudaka et al (1969, p. 11),who found that each vegetation type in a Pacific coast peatland ecosystem had its own micro-climate, with maximum and minimum temperatures more extreme in bog and swamp than in surrounding forest and transition zones. Rigg (1947, p. 468) and Williams (1968, p. 196) also found that minimum temperatures were lower in a bog than in surrounding upland regions.

4. Biotic influence

Man has a continuous influence on the peatland ecosystem situated southwest of Elma. The presence of the Whitemouth municipality garbage dump to the north, separated from direct contact with the peatland by a series of now-abandoned gravel pits, and the presence of agricultural lands on the three remaining sides of the peatland, provide the opportunity for the addition of nutrients into the peatland through seepage and via air currents.

Some cutting of surface peat has occurred in a section to the south of the study area. Yet, this disturbance was far enough removed from the actual site of study that it was assumed to have no direct influence on any values of productivity or accumulation obtained.

On the study area itself, a surveying team (1968) left its mark with a series of felled trees and vehicle tracks. Animals

other than man, e.g., deer, rabbits, etc., have also developed a network of paths across the surface of the study area. These disturbed areas were avoided when vegetation was sampled.

Due to this large array of disturbances the adjective "pristine" could never be applied to the peatland under study. Yet, in view of the present influence of man and his technology on ecosystems this site was still considered to be relatively natural.

C. Vegetation in areas adjacent to the peatland

Elma is found in a portion of the Great Lakes - St. Lawrence Forest Region, L-12, as denoted by Rowe (1959, p. 53).

> Low relief and poor drainage have favoured the development of extensive swamps, with Black Spruce (Picea mariana), tamarack (Larix laricina), eastern cedar (Thuya occidentalis), willow and alder scrub...Large areas of balsam poplar (Populus balsamifera), white spruce (Picea glauca), balsam fir (Abies balsamea) and scattered tamarack (Larix laricina) are found inland from the rivers...Trembling aspen (Populus temuloides) is common throughout the section. (Rowe, 1959, p. 53)

Deciduous wooded areas surrounding the peatland (Smith et al, 1967, Figure 6) have a tree cover composed primarily of Populus and Salix, with associated understory genera as described by Anderson (1960, p. 79-83), e.g., Cornus, Rosa, Ribes, Galium, Smilacina, Petasites, Fragaria, Maianthemum, Asarum.

# Chapter III

# REPRESENTATION OF NET PRIMARY PRODUCTION AND ACCUMULATION IN A PEATLAND

The second step in this study involved the construction of a scheme to represent first, the distribution of dry matter resulting from net primary production in various plant components, and second, the amount of this dry matter which is incorporated into peat (Figure 4).

The following pages indicate the sequential procedure used in attaching numerical values to most components in this scheme. At each step in the construction process values calculated in the present study are compared to corresponding literature values. Conclusions as to the significance of the observed values are noted in a discussion included with each section, since the volume of data involved is too great to be handled efficiently in a general discussion.

With the assignment of numerical values to all possible components in the above scheme, conclusions formed from the observed relationship between the processes of production and accumulation in the peatland studied, are summarized in Chapter IV.

Figure 4. The distribution of dry matter resulting from net primary production.

$A_f$ = peat formed in previous growing seasons

$A_i$ = material accumulated in the current growing season

$A_i'$ = material remaining after one year of decomposition

$A_f'$ = peat remaining after an additional year of decomposition

$A_t'$ = total peat remaining after a year of decomposition

$Cb_n$ = plant component produced in a previous growing season

$Cb_n'$ = plant component produced in a previous growing season and lost through death during the current growing season

$Cc_p$ = current production lost through herbivore consumption

$Cp_n$ = plant component contributing to the production of dry matter

$Cp_n'$ = plant component produced during the current growing season but lost through death

$FFb_2$ = flower-fruit produced in previous growing seasons

$FFp_3$ = flower-fruit produced in the current growing season

HV = solar energy

I = inorganic raw materials required in the photosynthetic process

j = number of non-vascular species present

$K'$ = decomposition rate in litter produced in the current growing season

$K''$ = decomposition rate in peat formed in previous years and still subject to decomposition

$Lp_1$ = leaves and petioles produced in the current growing season

Figure 4. (continued)

$LSp_8$ = laterals, e.g., rhizomes, produced in the current growing season

$PLb_1$ = biomass of leaves and petioles produced in previous growing seasons

$PLp_2$ = current production in leaves and petioles produced in previous growing seasons

$PLSb_5$ = laterals, e.g., rhizomes, produced in previous growing seasons

$PRb_4$ = roots produced in previous growing seasons

$PSb_3$ = stems, and bark when present, produced in previous growing seasons

$Rp_6$ = roots produced in the current growing season

$RRp_7$ = current production in roots produced in previous growing seasons

$RSp_5$ = current production in stems produced in previous growing seasons

$Sc_p$ = current production lost through secretion, i.e., rainwater leaching and root exudates

$Sp_4$ = terminal stem, including bark when present, produced in the current growing season

$t$ = total number of species present

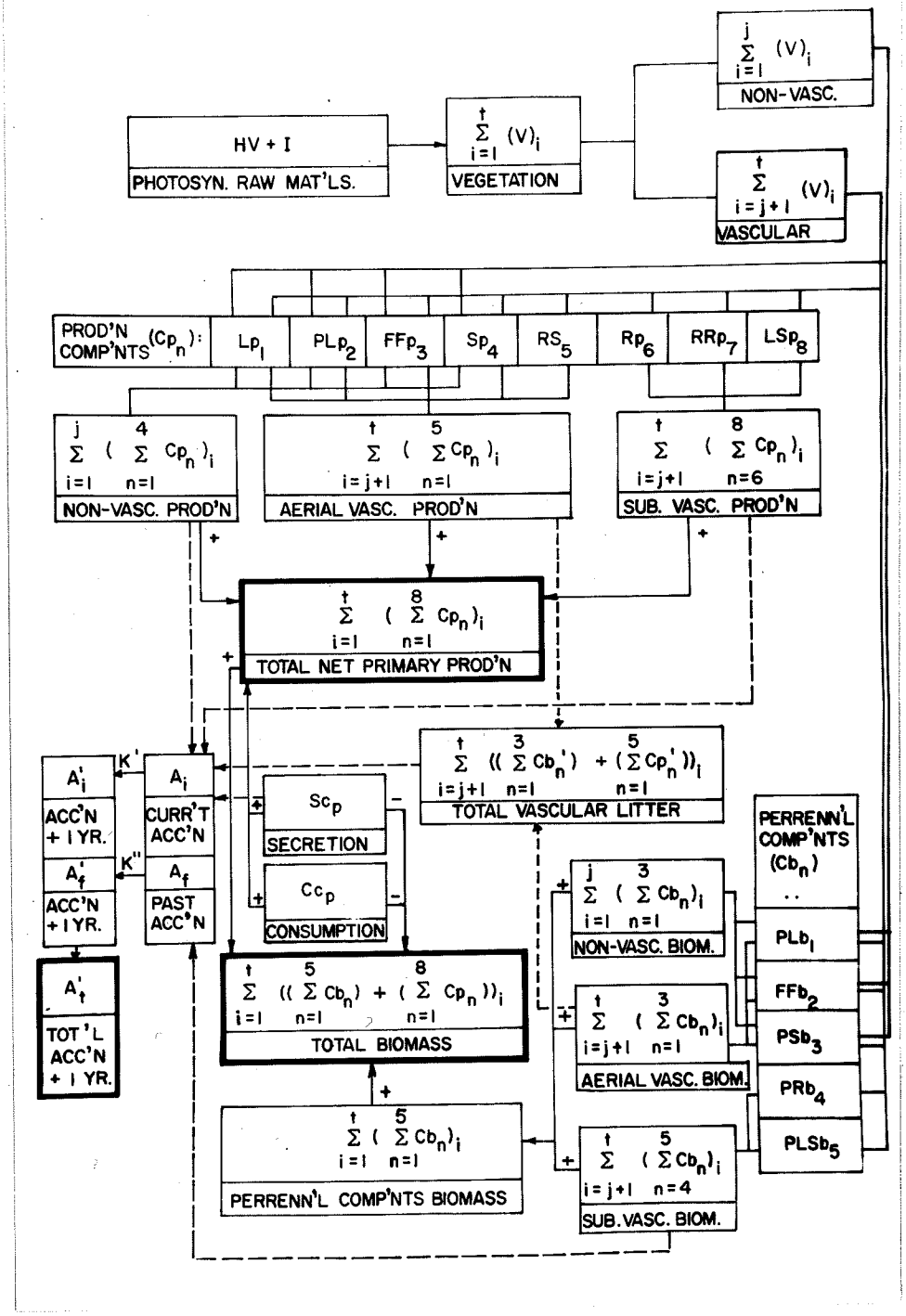
$v$ = a plant species

$\sum$ = sum

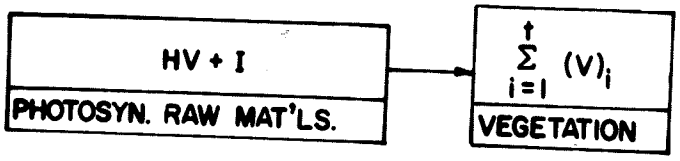
$+$ = addition

_____ = production process

_ _ _ _ _ = accumulation process


HV + I
PHOTOSYN. RAW MAT'LS.
$\sum_{i=1}^{t} (V)_i$
VEGETATION
$\sum_{i=1}^{j} (V)_i$
NON-VASC.
$\sum_{i=j+1}^{t} (V)_i$
VASCULAR
PROD'N COMP'NTS $(Cp_n)$:
$Lp_1$
$PLp_2$
$FFp_3$
$Sp_4$
$RS_5$
$Rp_6$
$RRp_7$
$LSp_8$
$\sum_{i=1}^{j} (\sum_{n=1}^{4} Cp_n)_i$
NON-VASC. PROD'N
$\sum_{i=j+1}^{t} (\sum_{n=1}^{5} Cp_n)_i$
AERIAL VASC. PROD'N
$\sum_{i=j+1}^{t} (\sum_{n=6}^{8} Cp_n)_i$
SUB. VASC. PROD'N
$\sum_{i=1}^{t} (\sum_{n=1}^{8} Cp_n)_i$
TOTAL NET PRIMARY PROD'N
$\sum_{i=j+1}^{t} ((\sum_{n=1}^{3} Cb_n') + (\sum_{n=1}^{5} Cp_n'))_i$
TOTAL VASCULAR LITTER
$A_i'$
ACC'N + 1 YR.
$A_f'$
ACC'N + 1 YR.
K'
K''
$A_i$
CURR'T ACC'N
$A_f$
PAST ACC'N
$Sc_p$
SECRETION
$Cc_p$
CONSUMPTION
$A_t'$
TOT'L ACC'N + 1 YR.
$\sum_{i=1}^{t} ((\sum_{n=1}^{5} Cb_n) + (\sum_{n=1}^{8} Cp_n))_i$
TOTAL BIOMASS
$\sum_{i=1}^{t} (\sum_{n=1}^{5} Cb_n)_i$
PERRENN'L COMP'NTS BIOMASS
$\sum_{i=1}^{j} (\sum_{n=1}^{3} Cb_n)_i$
NON-VASC. BIOM.
$\sum_{i=j+1}^{t} (\sum_{n=1}^{3} Cb_n)_i$
AERIAL VASC. BIOM.
$\sum_{i=j+1}^{t} (\sum_{n=4}^{5} Cb_n)_i$
SUB. VASC. BIOM.
PERRENN'L COMP'NTS $(Cb_n)$
$PLb_1$
$FFb_2$
$PSb_3$
$PRb_4$
$PLSb_5$

A. Vegetational patterns



1. Peatland vegetation

The whole peatland could not be subjected to analysis because of its large size, i.e., 140 hectares (Bannatyne, 1964, p. 16). The smaller area chosen for study (Figure 5) had the shape of a parallelogram, with a width of 150 meters (E-W) and a length of 250 meters (N-S).

(a) Past vegetation in the study area

To determine the sequence of previous vegetation types in the study area borings were made at each of the eight permanent sampling points used in productivity sampling and the peat profile examined at each point (Figure 6). The presence of gleyed clay at the bottom of each of the profiles indicated that the peatland had developed in a lake basin (Dachnowski, 1924, p. 107-108). In most cases, the entire profile was dominated by Sphagnum peat, often containing bits of wood and charcoal. A detailed analysis of the amorphous portions of the peat cores, similar to that carried out by Stewart & Durno (1969), would be required to determine the exact sequence of the hydrarch succession in the study area. To determine the average accumulation rate for existing peat reserves,three sampling points were chosen in the study area (ON 75E[1], 125N 75E, and 240N 75E), at which peat samples were collected

[1] Coordinate positions expressed with reference to Figure 5

Figure 5. Aerial view of the study area (infra-red ektachrome film). The study area is outlined in white, with co-ordinates expressed in meters.

I = Bog Forest zone

2 = Muskeg zone

3 = Bog zone

4 = Lagg zone

. = permanent sampling point

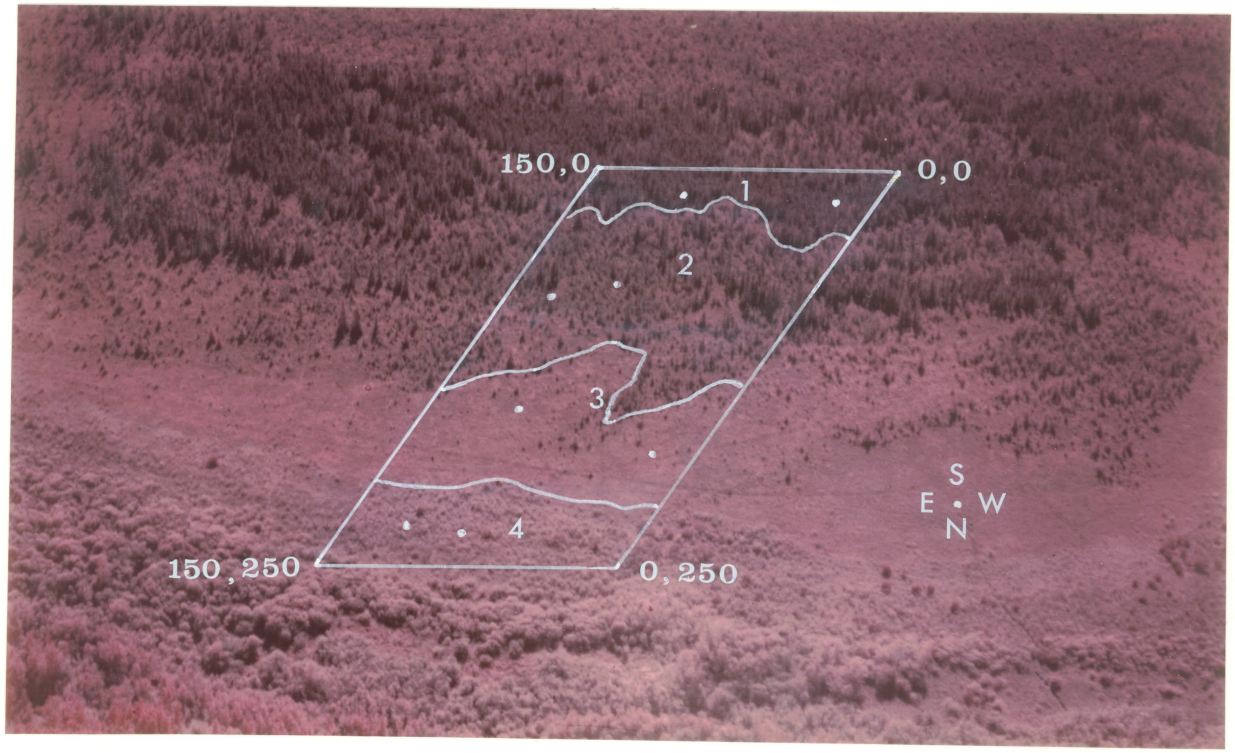

150,0
0,0
1
2
3
4
150,250
0,250
S
E
W
N

Figure 6. Peatland macrostratigraphy at eight selected points in the study area. The Munsell notation for colour appears in parenthesis.

1 = non-compacted peat-forming material

2 = dark brown (10YR 3/3), slightly-humified, Carex spp. fen peat, containing bits of wood

3 = very dark brown (10YR 2/2), well-humified, Carex spp. fen peat

4 = reddish yellow (7.5YR 7/8), non-humified, Sphagnum peat

5 = dark brown (7.5YR 3/2), slightly-humified, Sphagnum peat

6 = dark brown (7.5YR 3/2), slightly-humified, Sphagnum peat, containing bits of wood

7 = dark reddish brown (5YR 2/2), moderately-humified, Sphagnum peat

8 = dark reddish brown (5YR 2/2), moderately-humified, Sphagnum peat, containing bits of wood

9 = black (10YR 2/1), well-humified, amorphous peat

10 = black (10YR 2/1), well-humified, amorphous peat, containing bits of wood

11 = black (2.5YR 2/0), gleyed clay and peat

12 = light grey (7.5YR 7/0), gleyed clay

13 = wood

14 - quartz pebbles

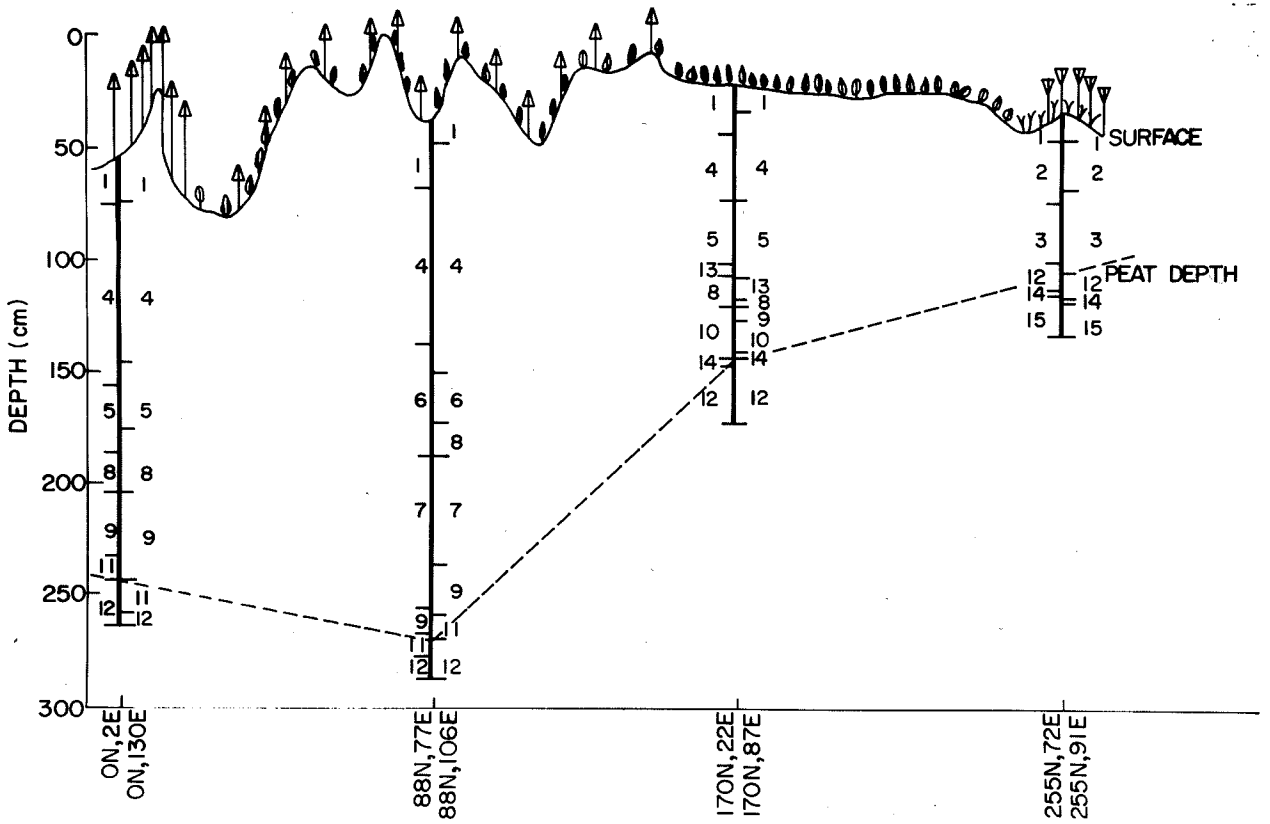
15 = quartz silt

Y = Gramineae and Cyperaceae

Y = Salicaceae

Φ = Ericaceae

Φ = Pinaceae




STUDY AREA SAMPLING POINT COORDINATES
WITH REFERENCE TO FIGURE 5 (meters North and East)

for radiocarbon dating. The macrostratigraphy at these points was similar to that indicated in Figure 6. The results of the dating, courtesy of the geology department, Brock University, are given in Table Ia. The age of the deepest samples collected indicated the peatland to be approximately 8,000 years old. This age falls midway between figures for peatland age determined for other parts of Canada by Nichols (1969, p. 63), reporting a maximum of 4,350 years B.P., and the figure of 11,000 years B.P. found to the beginning date for organic sedimentation in a northern Minnesota peatland tract by Heinselman (1970, p. 255).

As stated in the introduction, the actual rate of accumulation could be calculated from the following equation:

$$\Delta A_t = \frac{\text{total measured weight or height of peat present}}{\text{radiocarbon age of the total weight or height}}$$

The annual height increment calculated from these datings (Table Ia) ranged from 0.025 to 0.042 centimeters per year. This was less than the 0.048-0.062 centimeter per year range established by previous authors (Table IIa) for this same $47^{o}$-$49^{o}$N latitude.

The total weight of peat present per unit volume was determined by combining average height increment values, $\Delta A_t$ (height), with the dry weights of peat cores collected at each of the eight sampling points (Table Ib). This product provided an estimate of $\Delta A_t$ (weight), the average weight of peat accumulated

TABLE I

THE ANNUAL ACCUMULATION RATE OF RADIOCARBON-DATED PEAT

(A) ANNUAL WEIGHT INCREMENT AT THREE POSITIONS IN THE STUDY AREA

| Sample Point Coordinates | (a) Sample Depth cm. | Analysis Number | (b) Age in Years B.P. ± Standard Error | (a) ÷ (b) $\Delta A_t$ (height) cm./yr. |
|---|---|---|---|---|
| ON 75E | 185-190 | BGS-13B | 4524 ± 126 | 0.0408-0.0420 |
| 125N 75E | 200-205 | BGS-13C | 7939 ± 103 | 0.0252-0.0258 |
| 240N 75E | 80-85 | BGS-13A | 2960 ± 73 | 0.0270-0.0287 |

(B) DRY WEIGHT OF PEAT FOUND AT EIGHT SAMPLING POINTS IN THE STUDY AREA

| Sample point coordinates | Total peat depth cm. | Peat dry weight (105°C) gm./m.$^2$/cm. | Mean weight closest to radiocarbon-dating points gm./m.$^2$/cm. |
|---|---|---|---|
| ON 2E | 159 | 844.5 | 876.9 |
| ON 130E | 172 | 909.4 | |
| 88N 77E | 201 | 1218.0 | 1051.5 |
| 88N 106E | 212 | 1006.9 | |
| 170N 22E | 102 | 990.6 | |
| 170N 87E | 111 | 990.6 | |
| 255N 72E | 55 | 1624.0 | 1851.4 |
| 255N 91E | 60 | 2078.7 | |

(C) ANNUAL WEIGHT INCREMENT AT THREE POSITIONS IN THE STUDY AREA

| Sample point coordinates | (a) Height increment cm./yr. | (b) Mean weight closest to radiocarbon-dating points gm./m.$^2$/cm. | (a)(b) $\Delta A_t$ (weight) gm./m.$^2$/yr. |
|---|---|---|---|
| ON 75E | 0.0414 | 876.9 | 36.3 |
| 125N 75E | 0.0255 | 1051.5 | 26.8 |
| 240N 75E | 0.0279 | 1851.4 | 51.7 |

TABLE II

(A) PREVIOUS ESTIMATES OF THE ACCUMULATION RATE OF PEAT (HEIGHT)

| Investigator | Height Increment cm./yr. | Location | Technique Employed | Depth of Peat cm. |
|---|---|---|---|---|
| Durno (1961) | 0.012-0.015 | 57°N England | C-14* | 200-680 |
| Turner (1964) | 0.035-0.065 | 52°N England | C-14 | 88-173 |
| Tsukada (1967) | 0.036-0.093 | 36°-38°N Japan | C-14 | 775 |
| Heinselman (1961) (1963) | (i) 0.048<br>(ii) 0.33-0.41 | 48°N Minnesota | (i) C-14<br>(ii) dated tree roots | (i) 215<br>(ii) 37-50 |
| Rigg & Gould (1957) | 0.062 | 47°-49°N Washington | C-14 | 689 |
| Sears & Janson (1933) | (i) 0.076-0.13<br>(ii) 0.060-0.30 | 40°N Ohio | (i) dated conifer needles<br>(ii) Literature survey | 732 |
| Heilman (1968) | 0.22-0.38 | 65°N Alaska | C-14 | 41-71 |
| Leisman (1953) (1957) | (i) 1.50<br>(ii) 1.40 | 47°N Minnesota | (i) dated tree seedlings<br>(ii) buried wire | -<br>- |

*radiocarbon dating the basal portion of a core of known height

TABLE II (continued)

(B) PREVIOUS ESTIMATES OF THE ACCUMULATION RATE OF PEAT (WEIGHT)

| Investigator | Weight Increment gm./m.$^2$/yr. | Location | Technique Employed | Surface Vegetation Type |
|---|---|---|---|---|
| Johnson & Durnham (1963) | 72-100 | 54°N England | C-14 | blanket-raised bog |
| Gore & Olson (1967) | 97 | 54°N England | computer simulation based on productivity measurements | valley and blanket bog |
| Heilman (1968) | 150-280 | 65°N Alaska | C-14 | muskeg |

annually during the entire peat forming period (Table Ic).

Since $\Delta A_t$ (height) values were less than average values reported previously, then it was not surprising that the range of $\Delta A_t$ (weight) values, 26.8-51.7 gm./m.$^2$/yr., was also much lower than the 72-280 gm./m.$^2$/yr. range previously established (Table IIb).

The occurrence of past fires in the area, destroying upper peat layers, was indicated by the presence of a small amount of charcoal in the cores examined. These fires may be responsible for the lower than average rate of accumulation observed. Differences in the peat types present, and in past environments at the site should also be considered when attempting to relate long term accumulation values derived from the cores to current rates of production and accumulation.

(b) Present surface vegetation

The composition and spatial distribution of surface vegetation must be known before one can determine which species make the greatest contribution to production.

Species found on the peatland surface at Elma (Appendix A) have previously been identified in peatlands on the Pacific coast (Rigg, 1925, p. 266; Tsudaka et al, 1969, p. 5-7), through Alberta (Moss, 1953, p. 461-464), Saskatchewan (Jeglum, 1968, p. 203-214), Manitoba (Ritchie, 1956, p. 547-551), Minnesota (Heinselman, 1963, p. 334-335), northern Ontario (Wilde et al, 1954, p. 35), Michigan (Gates, 1942, p. 239), Quebec (Dansereau and Segadas-Vianna, 1952, p. 510-517), and Nova Scotia (Bell and Burchell, 1955, p. 548). These peatland species are distributed in two planes:

(i) horizontal: i.e., the length and width of the area

(ii) vertical: i.e., position relative to a fluctuating water table, plus relative height of aerial plant portions.

(1) Horizontal distribution of vegetation in the study area

To determine the range of species found in the study area, five 250 m. N-S line transects were set out at regular 30 m. intervals, including the entire width of the study area. Along one of these transects, species found either above, below, or touching

a piece of nylon line were recorded in one meter intervals for a total length of 262 m. The range of species encountered was then compared graphically (Figure 7). The substantial amount of range overlap among species so plotted, indicated the continuously changing nature of total species composition along the length (N-S) of the study plot.

On the remaining four transects the presence or absence of species was determined at intervals of 10 m. By comparing the total frequency of occurrence by a species on each of these transects, changes in the composition of vegetation at various widths in the study area could be determined. Since results indicated an absence of any well-defined trends or changes over the 150 m. width, it was concluded that vegetation composition was uniform in this direction. Aerial photographs had previously suggested the same conclusions; namely, that there existed four concentric patterns of vegetation radiating outwards from some unknown epicentre in the peatland (Figure 8). These concentric zones have been arbitrarily delimited as follows:

Zone 1: Bog Forest[1]: an area of closed-canopy trees (Picea mariana), few understory herbs or shrubs,

---

[1] See Appendix C for definition

Figure 7. The range of species along a single line transect. Nomenclature is that of Scoggan (1957) for vascular species, and of Crum et al (1965) for non-vascular species (Appendix A).

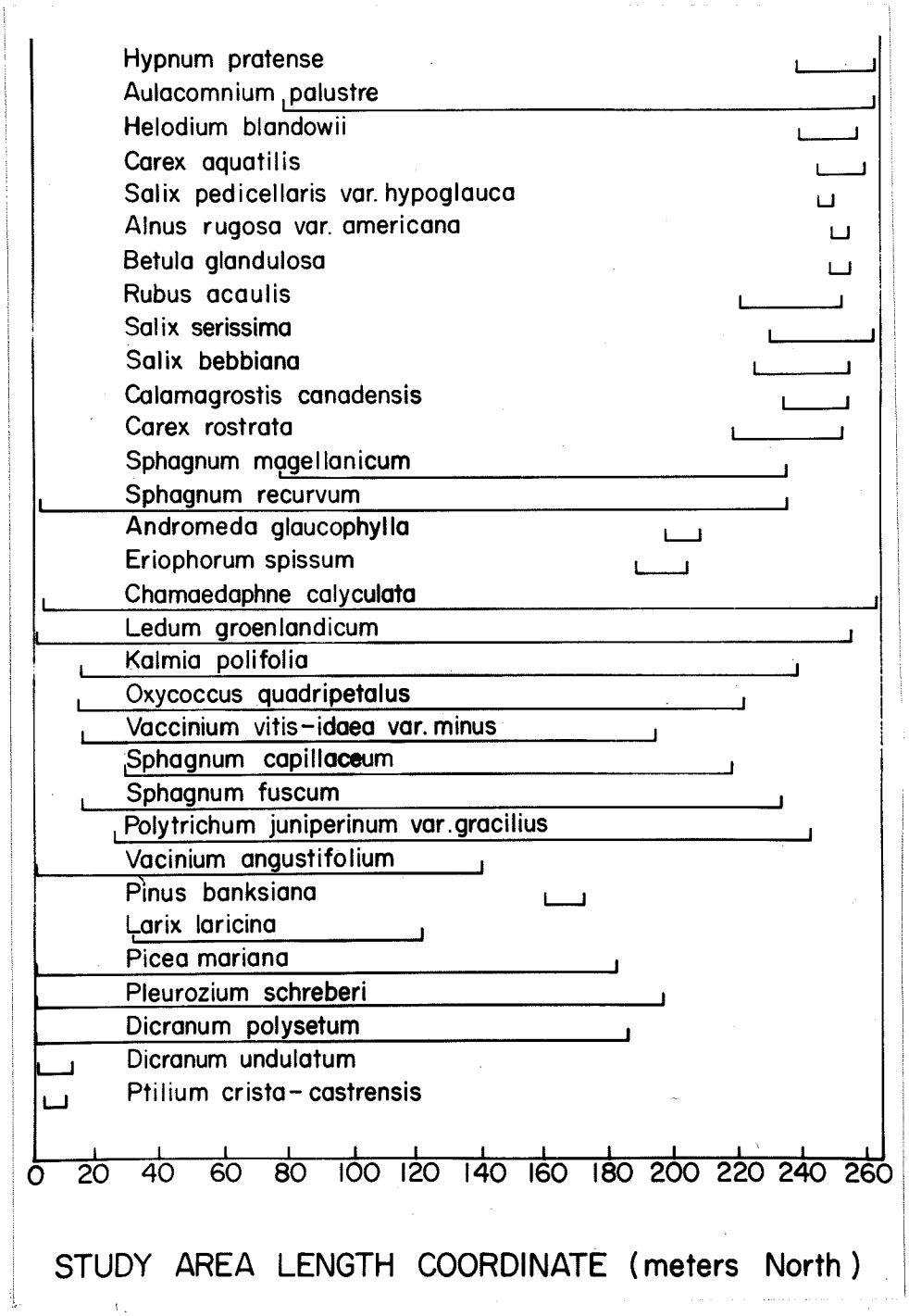

Hypnum pratense
Aulacomnium palustre
Helodium blandowii
Carex aquatilis
Salix pedicellaris var. hypoglauca
Alnus rugosa var. americana
Betula glandulosa
Rubus acaulis
Salix serissima
Salix bebbiana
Calamagrostis canadensis
Carex rostrata
Sphagnum magellanicum
Sphagnum recurvum
Andromeda glaucophylla
Eriophorum spissum
Chamaedaphne calyculata
Ledum groenlandicum
Kalmia polifolia
Oxycoccus quadripetalus
Vaccinium vitis-idaea var. minus
Sphagnum capillaceum
Sphagnum fuscum
Polytrichum juniperinum var. gracilius
Vacinium angustifolium
Pinus banksiana
Larix laricina
Picea mariana
Pleurozium schreberi
Dicranum polysetum
Dicranum undulatum
Ptilium crista-castrensis
0 20 40 60 80 100 120 140 160 180 200 220 240 260
STUDY AREA LENGTH COORDINATE (meters North)

Figure 8. The concentric nature of vegetation patterns. Some snow still remains in treed areas (May, 1970).

and a "feather-moss" substratum. (Type 5, Heinselman, 1970, p. 242).

Zone II: Muskeg: a transition area combining elements of the Bog and Bog Forest zones. It is characterized by a canopy of coniferous trees (P. mariana), between which are found clumps of ericaceous shrubs rooted in a bryophyte substratum. (Type 6, Heinselman, 1970, p. 242).

Zone III: Bog: a treeless area dominated by ericaceous shrubs rooted in a bryophyte substratum composed mainly of Sphagnum spp. (Type 7, Heinselman, 1970, p. 242).

Zone IV: Lagg: peripheral area of the peatland characterized by forbs, e.g., Carex spp., and by deciduous shrubs, e.g., Salix spp. .

While the continuously variable nature of vegetation composition along the length (N-S) of the study area made it difficult to define the boundaries of these four zones, differences in the degree and type of tree cover present allowed the zones to be distinguished in aerial photographs, e.g., Figure 5.

These same zones could also be thought of as a series of seral stages in the process of succession. According to Moss

Figure 9. Vegetation in Zone I : Bog Forest

(a) Looking into the closed-canopy Picea mariana from the Muskeg zone (July, 1970). Black and white bands of the marker pole are each 20 cm. in length.

(b) Understory vegetation in the Bog Forest zone, consisting primarily of Ledum groenlandicum and Vaccinium angustifolium, with a continuous carpet of Pleurozium schreberi beneath (May, 1970). Marker pole colour band = 20 cm.

Figure 10. Vegetation in Zone II : Muskeg

(a) Widely-spaced Picea mariana (March, 1970).

(b) Understory shrubs consisting mainly of Ledum groenlandicum (July, 1970). Marker pole colour band = 20 cm.

Figure 11. Vegetation in Zone III : Bog

(a) Treeless bog mat composed of ericaceous shrubs rooted in a bryophyte substratum. Muskeg zone is in the background (July, 1970).

(b) Close-up of the bog surface, with Ledum groenlandicum, Vaccinium vitis-idaea var. minus, and Sphagnum fuscum visible (June, 1970). Marker pole colour band = 20 cm.

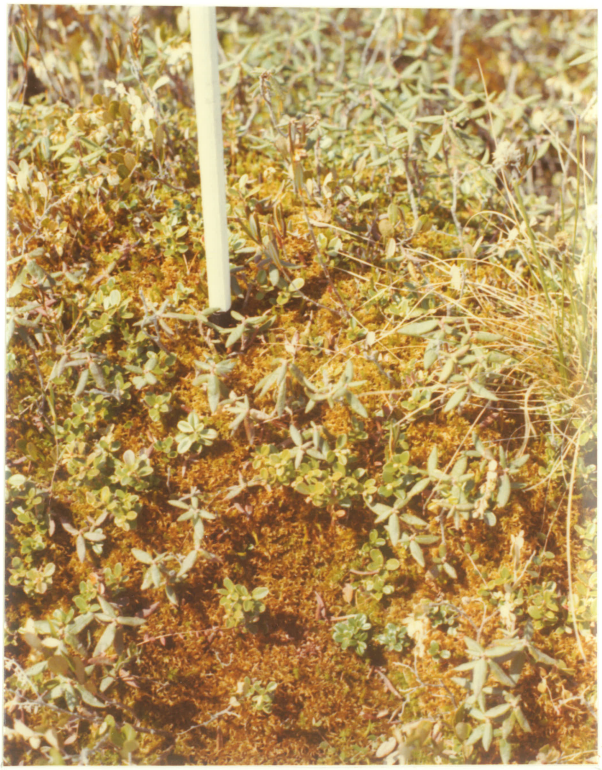


Figure 12. Vegetation in Zone IV : Lagg

(a) Shrub overstory, composed mainly of Salix spp., with Carex spp. visible beneath (August, 1970). Marker pole colour band = 20 cm.

(b) Carex rostrata and Chamaedaphne calyculata form the dominant understory vegetation (August, 1970). Marker pole colour band = 20 cm.

(1953a, p. 222) the Picea mariana - "feather moss" association, i.e., Bog Forest, may be interpreted as the edaphic climax in this process. However, this natural climax may be offset by burning, which causes retrogression to earlier stages of the sere (Moss and Turner, 1961, p. 1191).

The sporadic pattern of mature black spruce, deep indentations of Bog-type vegetation into the treed Muskeg portion, and evidence of charcoal in peat cores, all suggested that the distribution of present surface vegetation had been determined by the occurrence of past fires in the study area. The existing vegetation patterns therefore represent seral stages in the process of secondary succession.

Having classified the vegetation present into four types, the aim of the current study could be restated as: first, to calculate annual net primary production in each of the four successional zones defined above, and second, to establish what fraction of this production was accumulated annually as peat. The relationships between net primary production, subsequent peat accumulation, and time, represented by succession, were then numerically defined from the calculated values.

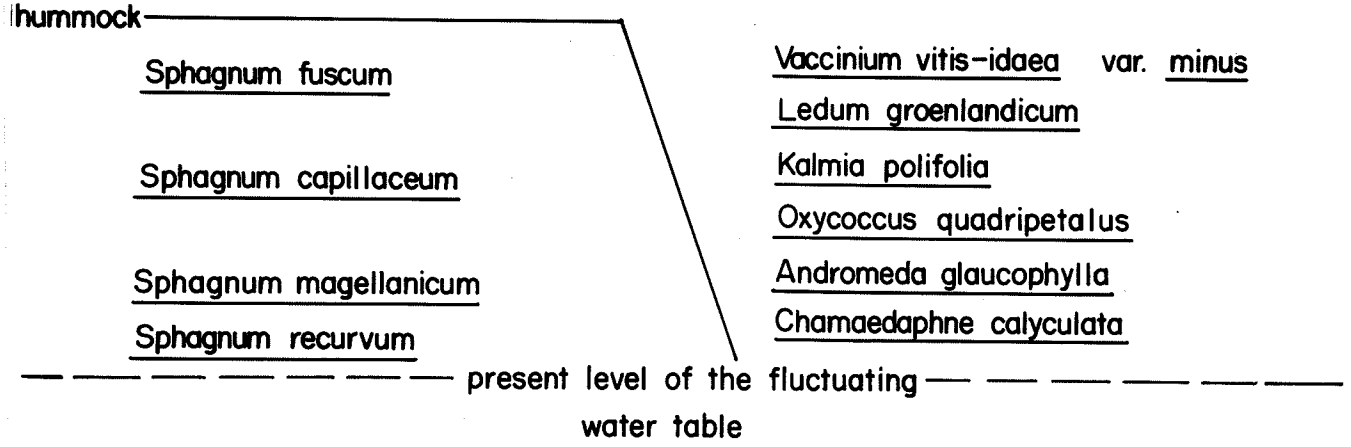
(2) Vertical distribution of vegetation in the study area

In the present study vegetation was considered to be composed of three strata: bryophyte and lichens; grasses, sedges,

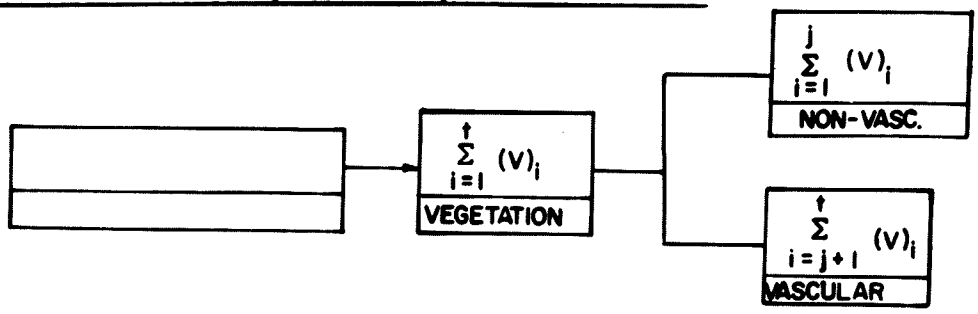
herbs, and shrubs less than breast height (1.3 m.) at maturity; and trees, including saplings of the same species, greater than 1.3 m. in height at maturity. This arbitrary division was found useful in constructing a sampling scheme to measure net primary production in each of the four previously defined peatland zones.

The vertical distribution of peatland species with regard to their position above a fluctuating water table was documented by Tansley (1939, p. 688) as a hummock-hollow "regeneration complex". The relative positions of hummock species on the peatland understudy (Figure 13) agreed with their representation given by Moss (1953, p. 467) for peatlands in Alberta.

Figure 13. Vertical distribution of hummock species on the surface of the peatland located southwest of Elma. The relative position of the water table at the start of the growing season is shown.


hummock
Sphagnum fuscum
Sphagnum capillaceum
Sphagnum magellanicum
Sphagnum recurvum
Vaccinium vitis-idaea var. minus
Ledum groenlandicum
Kalmia polifolia
Oxycoccus quadripetalus
Andromeda glaucophylla
Chamaedaphne calyculata
present level of the fluctuating water table

B. Determination of the most productive species in each zone



Relative frequency values were calculated for each of the species present in the four vegetation zones to determine which of the species made the most important contribution to production. The species which either touched, or were above a 3 mm. diameter piece of wire were recorded at 50 points in each zone. These points were equally spaced within the 150 m. width (E-W) of the study area. Frequency and relative frequency was determined for each species encountered in this exercise using the following equations:

$$\text{frequency} = \frac{\text{number of points at which a species occurred}}{\text{50 points}}$$

$$\text{relative frequency (\%)} = \frac{\text{species' frequency value}}{\text{total frequency for all species}} \times 100$$

An arbitrary value of 5% was used to distinguish between important ($\geq$ 5%) and less important ($<$ 5%) species. Only species having at least a 5% relative frequency value were considered on an individual basis in the calculation of net primary production.

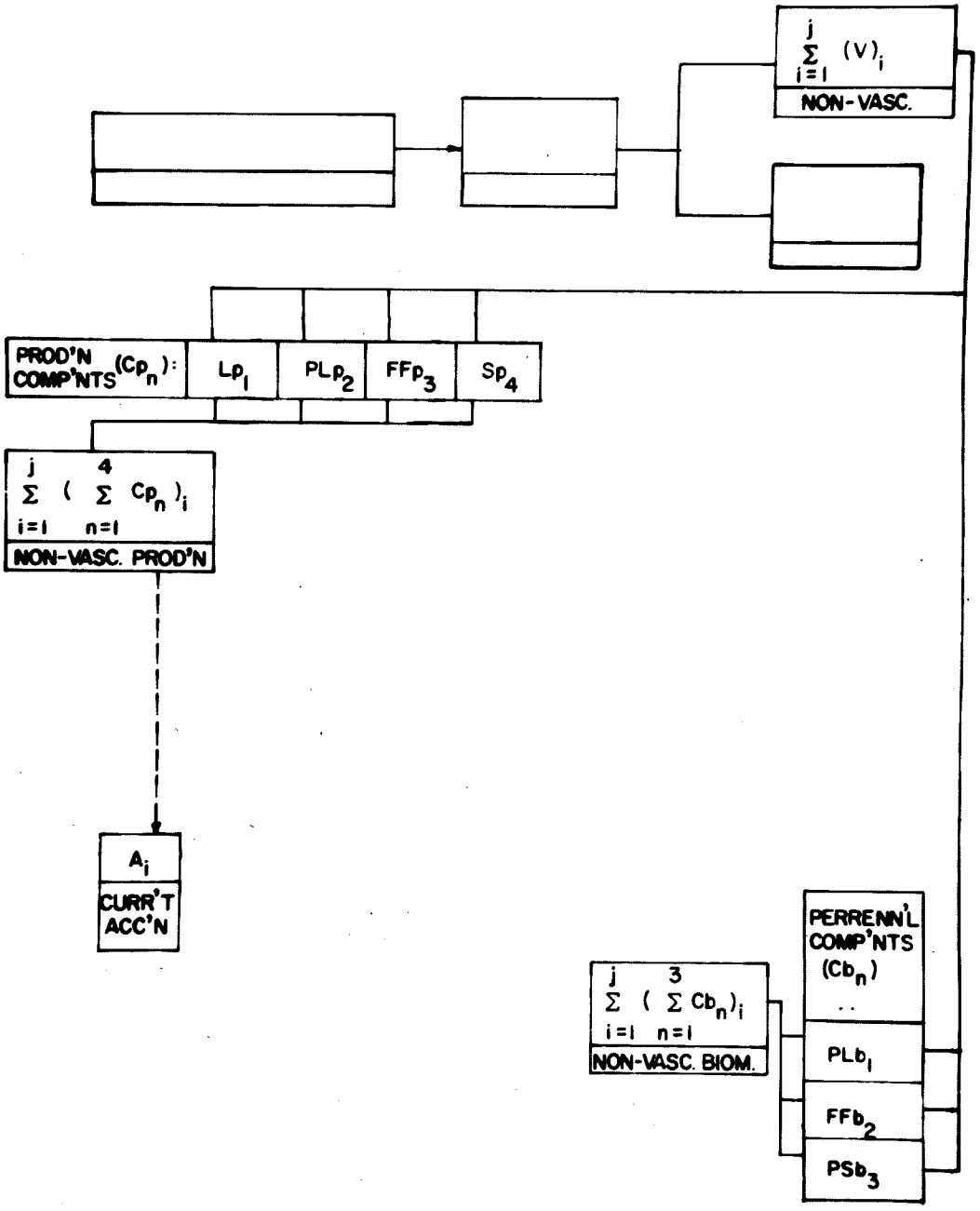
The results (Table III) indicated that relatively few species formed the bulk of vegetation present, with several of these species being important in more than just one zone. The fact that rankings of relative importance changed from zone to zone for overlapping species substantiated the view that there existed a "vegetation continuum" along the length of the study area.

TABLE III

RELATIVE FREQUENCY VALUES OF SPECIES FOUND IN EACH OF THE FOUR VEGETATION ZONES

| Zone | Important Species (relative frequency values $\geq$ 5%) | | Less Important Species (relative frequency values < 5%) | |
|---|---|---|---|---|
| | Species | Value % | Species | Value % |
| Bog Forest | Ledum groenlandicum | 30.3 | Vaccinium vitis-idaea var. minus | 4.1 |
| | Picea mariana | 23.7 | Sphagnum fuscum | 4.1 |
| | Pleurozium schreberi | 22.9 | Cladonia spp. | 3.3 |
| | | | Chamaedaphne calyculata | 3.2 |
| | | | Vaccinium angustifolium | 2.5 |
| | | | Dicranum polysetum | 2.5 |
| | | | Sphagnum recurvum | 1.7 |
| Muskeg | Ledum groenlandicum | 28.6 | Cladonia spp. | 4.0 |
| | Picea mariana | 14.6 | Polytrichum juniperinum var. gracilius | 3.2 |
| | Sphagnum fuscum | 14.6 | Oxycoccus quadripetalus | 3.1 |
| | Chamaedaphne calyculata | 10.0 | Vaccinium angustifolium | 1.6 |
| | Vaccinium vitis-idaea var. minus | 9.3 | Pleurozium schreberi | 1.6 |
| | Kalmia polifolia | 5.4 | Sphagnum capillaceum | 0.8 |
| | | | Sphagnum magellanicum | 0.8 |
| | | | Ptilium crista-castrensis | 0.8 |
| | | | Aulacomnium palustre | 0.8 |
| | | | Dicranum polysetum | 0.8 |
| Bog | Chamaedaphne calyculata | 18.6 | Picea mariana | 2.4 |
| | Polytrichum juniperinum var. gracilius | 15.0 | Pinus banksiana | 1.8 |
| | Sphagnum fuscum | 14.4 | Cladonia spp. | 1.6 |
| | Ledum groenlandicum | 13.2 | Sphagnum capillaceum | 1.3 |
| | Oxycoccus quadripetalus | 9.6 | Sphagnum recurvum | 1.3 |
| | Vaccinium vitis-idaea var. minus | 7.8 | Sphagnum magellanicum | 0.8 |
| | Kalmia polifolia | 6.0 | Eriophorum spissum | 0.8 |
| | Aulacomnium palustre | 5.4 | | |
| Lagg | Chamaedaphne calyculata | 27.8 | Carex aquatilis | 4.5 |
| | Carex rostrata | 13.5 | Ledum groenlandicum | 3.7 |
| | Aulacomnium palustre | 12.0 | Rubus acaulis | 2.6 |
| | Hypnum pratense | 8.2 | Polytrichum juniperinum var. gracilius | 2.1 |
| | Calamagrostic canadensis | 7.5 | Sphagnum recurvum | 2.1 |
| | Salix bebbiana | 6.7 | Helodium blandowii | 1.4 |
| | Salix serissima | 5.2 | Betula glandulosa var. glandulifera | 0.9 |
| | | | Alnus rugosa var. americana | 0.9 |
| | | | Salix pedicellaris var. hypoglauca | 0.9 |

C. Biomass, net primary production, and subsequent accumulation of non-vascular vegetation



1. Sampling scheme

Of all non-vascular species found in the study area only those indicated in Table IV were considered to be important contributors to production. Calculation of net primary production for each of these species was carried out according to the scheme previously outlined in the introduction. That is, a number of individuals of each species were harvested at regular monthly intervals throughout the 1970 growing season, from which the weight of new growth per individual was determined.

Samples were collected from two random points in each of the four vegetation zones. At each of the eight points a linear series (E-W) of 25x25 cm. quadrats was set up, with the random point serving as origin. The use of 625 $cm.^2$ areas in production sampling was based on the results of a "species-area" investigation in which nested areas ranging in size from 25x25 cm. to 50x100 cm. were surveyed for both vascular and non-vascular species present. The "minimum area" of 625 $cm.^2$ was found to have each of the desired species occurring consistently. The number of such 25x25 cm. quadrats harvested at each sampling date was determined by the density of species present. A minimum of 80 individuals per species per zone was required to give a production estimate with a standard error no greater than ± 10% (the level of accuracy suggested by Milner & Elfyn Hughes (1968, p. 12) for

TABLE IV

IMPORTANT NON-VASCULAR SPECIES

| Species | Bog Forest | Muskeg | Bog | Lagg |
|---|---|---|---|---|
| *Pleurozium schreberi* | + | | | |
| *Sphagnum fuscum* | | + | + | |
| *Polytrichum juniperinum* var. *gracilius* | | | + | |
| *Aulacomnium palustre* | | | + | + |
| *Hypnum pratense* | | | | + |

productivity measurements).

At each monthly sampling date at least 80 individuals of each species were harvested from 625 $cm.^2$ areas in each zone, placed in polyethylene bags, and returned to the laboratory. Since the non-vascular plants were relatively small, the separation of current from old growth had to be done for each of the individuals included in the sample. In each of the following species this separation was performed under a binocular microscope, at a magnification of 6x.

Aulacomnium palustre

Since the leaves of this species remain green for more than one year[1] (personal observation), then the total length of the chlorophyllous portion of a plant cannot be equated with new growth. While Tamm (1953, p. 13) considered one third to one half the length of the chlorophyllous portion to be indicative of new growth, in the present study the current year's light green growth could be distinguished from perennial green portions by sampling A. palustre at monthly intervals throughout the growing season.

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[1] As the contribution to production by perennial leaves of all bryophytes was considered to be negligible, no correction factor was employed for these perennial portions in calculations of productivity.

To include the contribution made to production by reproductive structures, samples employed during the growing season contained both fertile and sterile shoots. This sampling procedure was applied in the following species as well.

Polytrichum juniperinum var. gracilius

As suggested by Longton and Greene (1967, p. 306-310) current terminal growth was identified based on differences in leaf length in individual plants, shorter stem leaves being produced at the beginning and end of a growing season.

Sphagnum fuscum

Of the three erect-growing genera examined, differentiation of new growth from old was found most difficult in this genus. Growth chamber studies, and subsequent field observations, confirmed the fact that in S. fuscum the stem portion of terminal new growth retained its chlorophyll for a single growing season only.

In this study, distinguishing between new growth and old was based simply on recognizing the boundary between green and brown pigment in a plant. Monthly samplings were made during the growing season to determine the maximum weight of the chlorophyllous portion.

Clymo (1970, p. 21) has recently suggested that some of the material in the capitulum of terminal new growth portions

is formed during previous growing periods. Following his suggestion, an average weight of the capitulum was determined at the onset of the growing season, and this mean weight subtracted from the total weight of individual terminal growth portions harvested throughout the remainder of the season. This procedure provided a more accurate value for current net production by an individual Sphagnum sp. plant.

Hypnum pratense[1]

Due to the proliferous branching system of this pleurocarpous moss, it was difficult to first define an "individual" for production purposes. For convenience, each unbranched segment having a growing point at its apex was referred to as an individual. Field observations indicated that these portions retained their chlorophyll for more than one year however, so that it was impossible to distinguish between new and old growth. The alternative taken was to determine the total weight of the green portion supporting a single growing point, i.e., the biomass, and to consider yearly net production per individual as one half this biomass value.

Pleurozium schreberi

While an individual was easier to define in this pleuro-

---

[1] Awaiting verification

carpous genus than in the former, it was still found impossible to distinguish between new and old terminal growth. Therefore, biomass figures obtained from monthly samplings were divided in half to approximate yearly net production (after Weetman, 1968, p. 368).

2. Net primary production of important non-vascular species

The new growth portions identified above, consisting of leaves, stems, and reproductive structures, were washed in distilled water to remove any extraneous material from their surfaces, and then oven-dried to constant weight at 105°C. After cooling in a desiccator, these individuals were weighed in groups of ten, with no effort being made to separate leaves, stems and reproductive structures. From these weights, a value for current net production per individual was obtained.

To calculate production of these species on an area basis, the value of current net production per individual was multiplied by the average density value determined for each species. The number of individuals per square centimeter was first calculated by counting the number of individuals found in either 6.5 or 9.5 cm. diameter plugs, usually containing a single species, and collected both in the winter when individuals were frozen into natural position, and in the spring when new growth buds were evident. At both collection dates plugs were gathered from all zones in which a species occurred. The number of plugs collected for each species was sufficient to give a density value having a standard error of less than 10%.

Next, the number of square centimeters occupied by each species in a square meter was calculated, employing a "gridded"

25x25 cm. quadrat. Each of the twenty-five 5x5 cm. areas contained therein were allotted a maximum cover value of 4%, with the total of the cover values recorded for a species representing the percent cover by that species. This procedure was repeated for a number of additional 25x25 cm. areas until a percent cover value with an acceptable standard error of estimate (< 10%) was obtained. The 25x25 cm. areas surveyed were located five meters south of each of the eight permanent sampling points, one half of the quadrats located at each zonal sampling point.

The product of the number of individuals per square centimeter and the number of square centimeters occupied by a species in a square meter (i.e., 100% cover = 10,000 square centimeters), provided an estimate of density for each of the important species. This density value, multiplied by the species' net production value per individual provided a value for net primary production on an area basis.

Net production values calculated for individual plants at monthly intervals over the growing season were plotted against time in Programme I. Due to the limited number of points, no conclusions were drawn concerning the shape of growth curves.

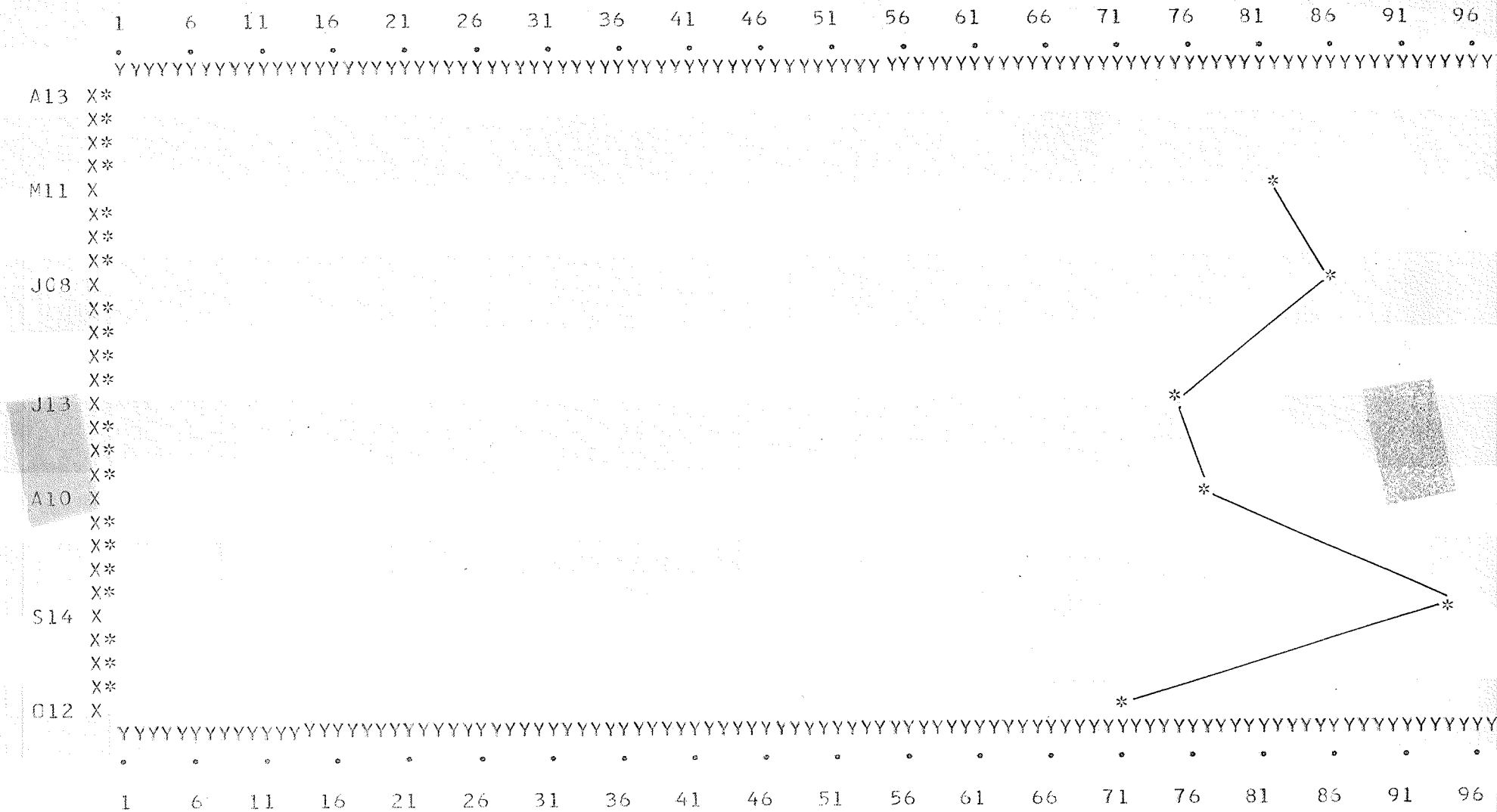
The significant difference in the individual production values of Sphagnum fuscum in the Bog versus the Muskeg zone, evident in the graphs of Programme I, suggested the existence

Programme I. Net primary production recorded at monthly intervals for individuals of each of the important non-vascular species studied during the 1970 growing season.

```
C  PROGRAMME 1
C------------
C
C  THIS PROGRAMME,WRITTEN IN WATFIV,GRAPHICALLY PRESENTS
C  THE PATTERN OF WEIGHT INCREMENT IN INDIVIDUALS
C  OF EACH OF THE IMPORTANT NON-VASCULAR SPECIES STUDIED
C
C  SOURCE PROGRAMME LISTING
C------------------------
C
      DIMENSION XLINE(100),IC2(27),LINE(100),YLINE(100)
      CHARACTER*10 $ZONE(7)
      CHARACTER*40 $SPEC(7)
      CHARACTER $P*4(8),$DATE*3(27)
      DATA $P/'NET ','PROD','UCTI','ON (','MGM)',' PER',' SHO','OT  '/
      DATA $DATE/'A13',' ',' ',' ',' ','M11',' ',' ',' ',' ','J08','
     *  ',' ',' ',' ',' ','J13',' ',' ',' ',' ','A10',' ',' ',' ','
     *  ',' ',' ','S14',' ',' ',' ',' ','O12'/
      DATA YAX/'Y'/,STAR/'*'/,BLANK/' '/,XAX/'X'/,$PER/'.'/
      N=7
      DO 9000 I = 1,N
      READ(5,6000) $ZONE(I),$SPEC(I)
 6000 FORMAT(A10,A40)
      READ(5,1600) (IC2(IT),IT=1,27),SCALE
 1600 FORMAT(20I4/7I4,F6.2)
 1141 WRITE(6,5000) $ZONE(I),$SPEC(I)
 5000 FORMAT('1',' ZONE:',A10,' SPECIES:',A40,' PRODUCTION GRAPH ')
      WRITE(6,100) $P
  100 FORMAT('0',45X,8A4)
      DO 222 L = 1,100,5
      LINE(L) = L
      YLINE(L) = $PER
  222 CONTINUE
      WRITE(6,121) (LINE(L),L=1,100,5)
  121 FORMAT('0',9X,20(I2,3X))
      WRITE(6,787) (YLINE(L),L=1,100,5)
  787 FORMAT(' ',9X,20(1X,A1,3X))
      DO 200 IP = 2,100,1
      XLINE(1) = BLANK
  200 XLINE(IP) = YAX
      WRITE(6,300) XLINE
  300 FORMAT(' ',9X,100A1)
      DO 400 IP = 1,100,1
  400 XLINE(IP) = BLANK
      KP = 27
      DO 700 JP = 1 ,KP
      XLINE(1) = XAX
      IP = IC2(JP) + 2
      XLINE(IP) = STAR
      WRITE(6,500) $DATE(JP),XLINE
  500 FORMAT(' ',4X,A3,1X,100A1)
      XLINE(IP) = BLANK
  700 CONTINUE
      DO 600 IP = 2,100,1
      XLINE(1) = BLANK
  600 XLINE(IP) = YAX
      WRITE(6,7000) XLINE
 7000 FORMAT(' ',9X,100A1)
```

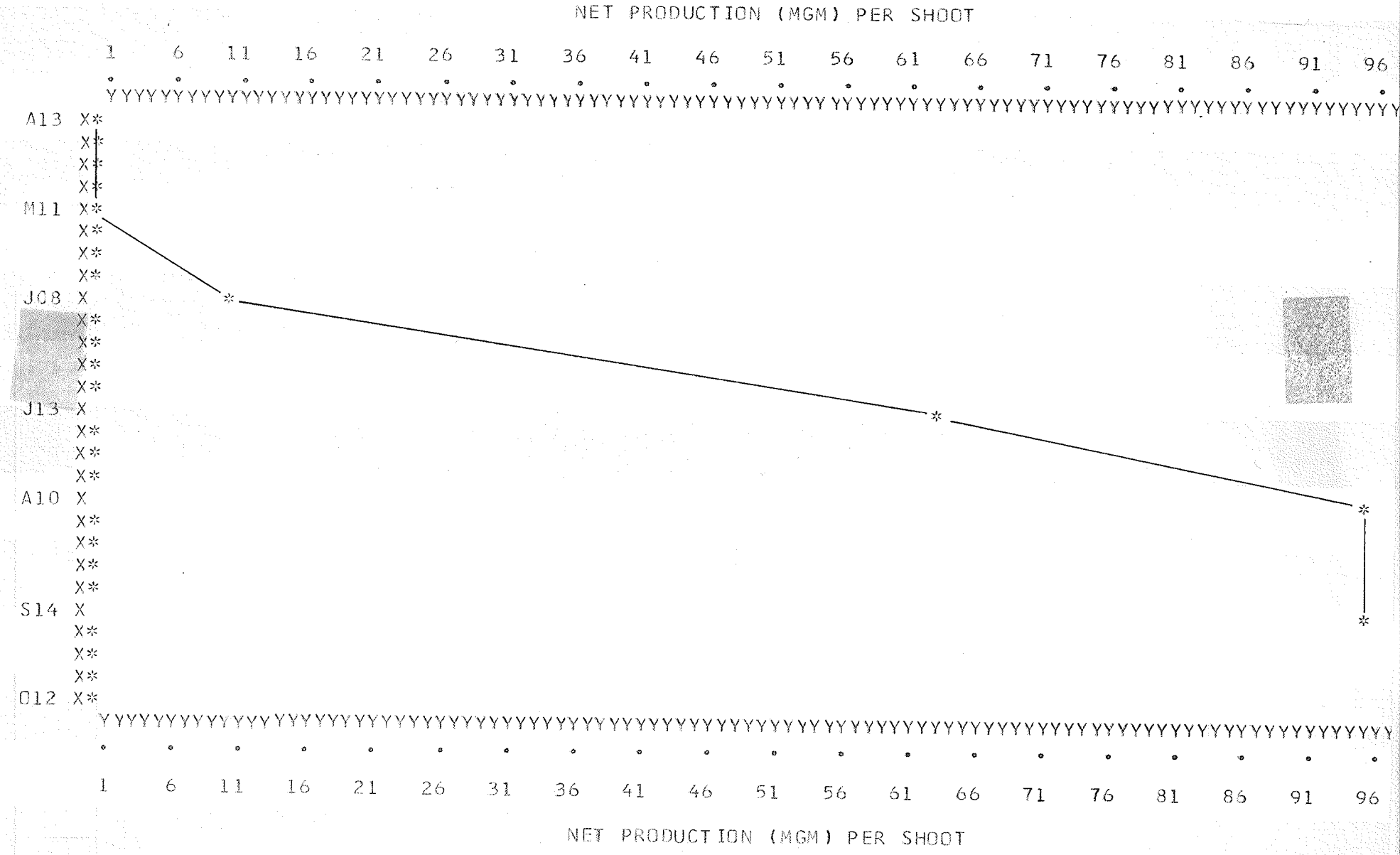
```
      DO 333 LL = 1,100,5
      LINE(LL) = LL
      YLINE(LL) = $PER
  333 CONTINUE
      WRITE(6,787) (YLINE(LL),LL=1,100,5)
      WRITE(6,121) (LINE(LL),LL=1,100,5)
      WRITE(6,800) $P
  800 FORMAT('0',45X,8A4)
  900 WRITE(6,1000) SCALE
 1000 FORMAT('-','NOTE:PRODUCTION IS ',F6.2,
     *' TIMES NUMBER OF Y''S INDICATED ON AXIS ')
 9000 CONTINUE
      STOP
      END
```

ZONE:BOG FOREST SPECIES:PLEUROZIUM SCHREBERI PRODUCTION GRAPH



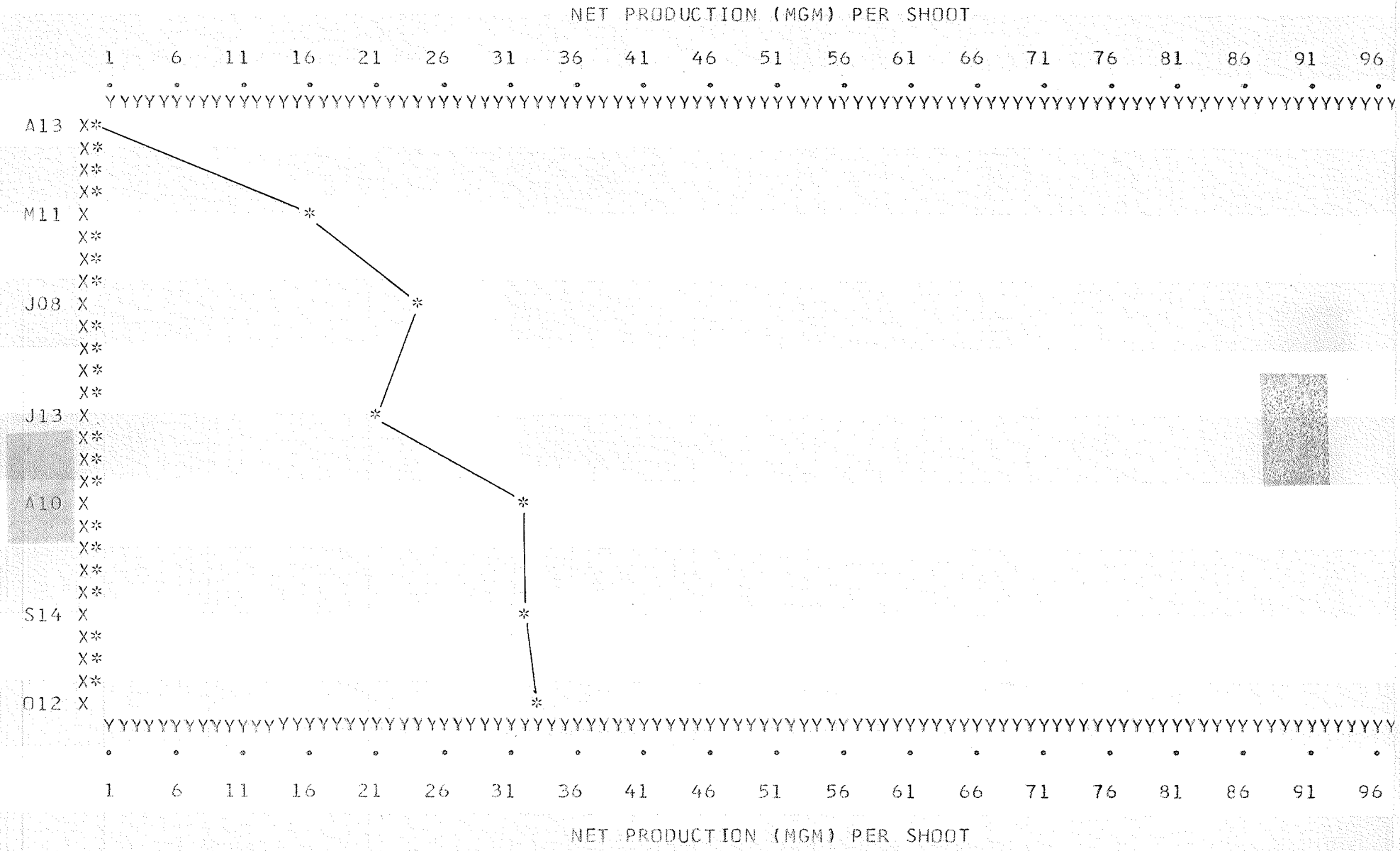

NOTE:PRODUCTION IS 0.05 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:MUSKEG SPECIES:SPHAGNUM FUSCUM PRODUCTION GRAPH



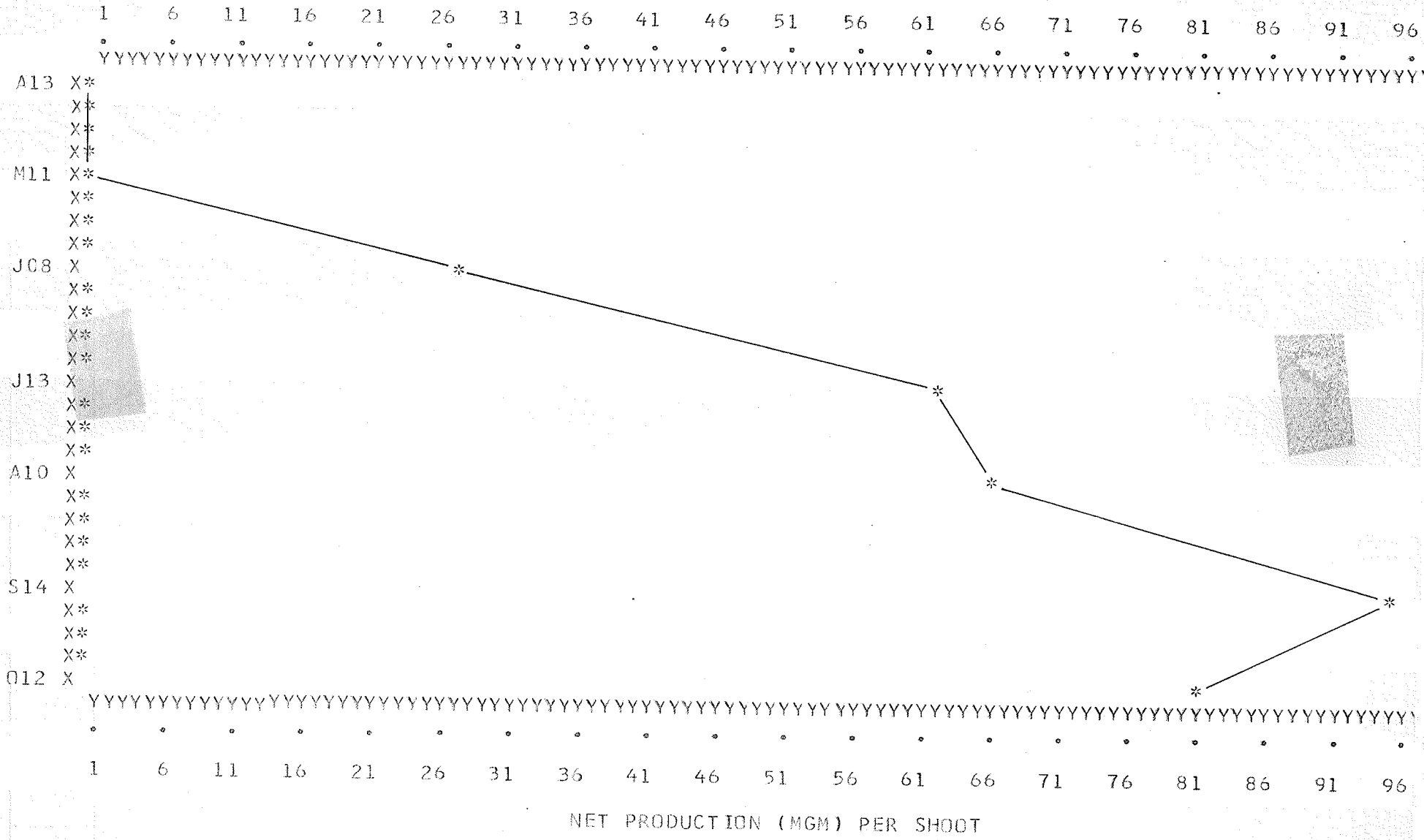

NOTE:PRODUCTION IS 0.01 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:BOG SPECIES:AULACOMNIUM PALUSTRE PRODUCTION GRAPH



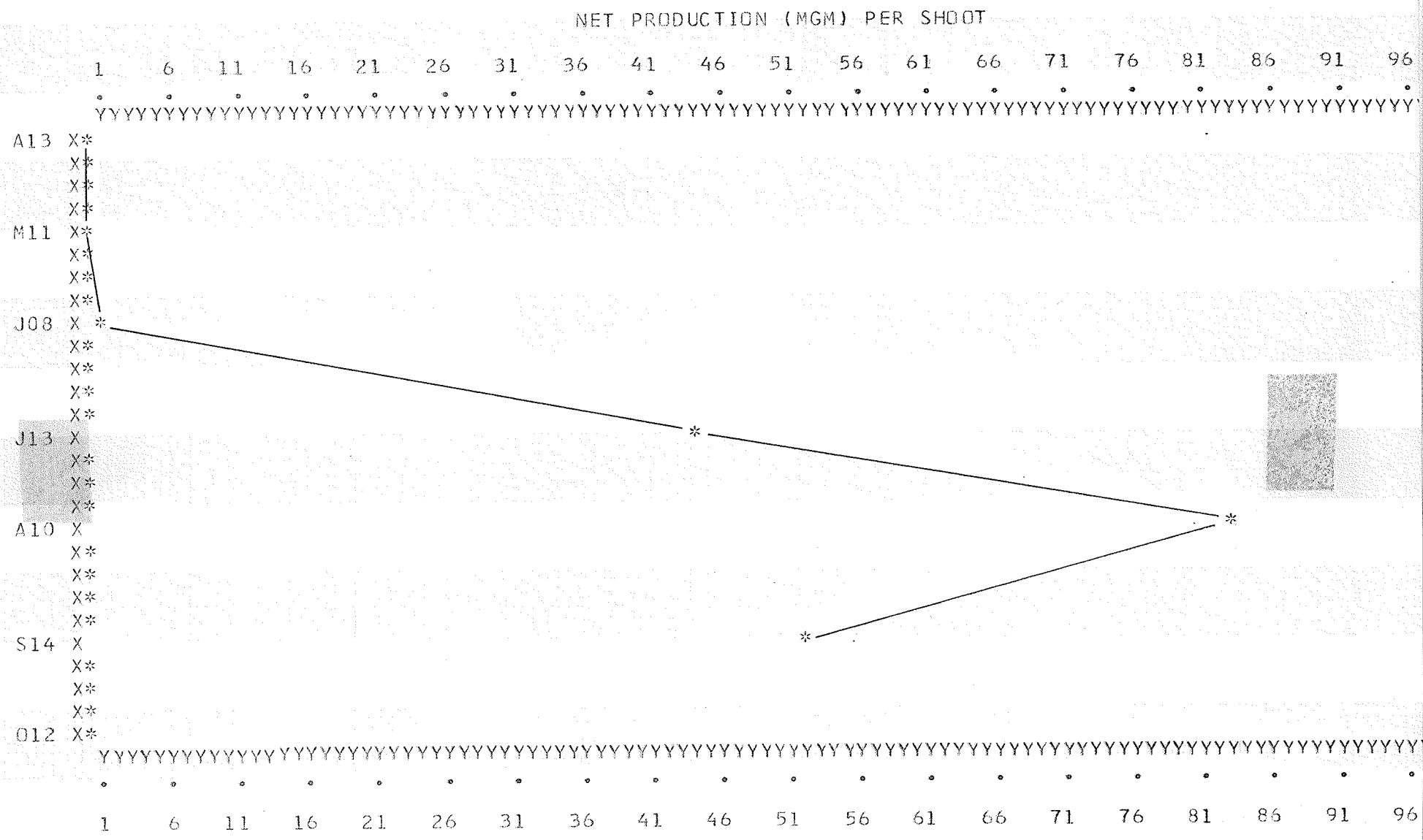

NOTE:PRODUCTION IS 0.03 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:BOG SPECIES:POLYTRICHUM JUNIPERINUM VAR. GRACILIUS PRODUCTION GRAPH



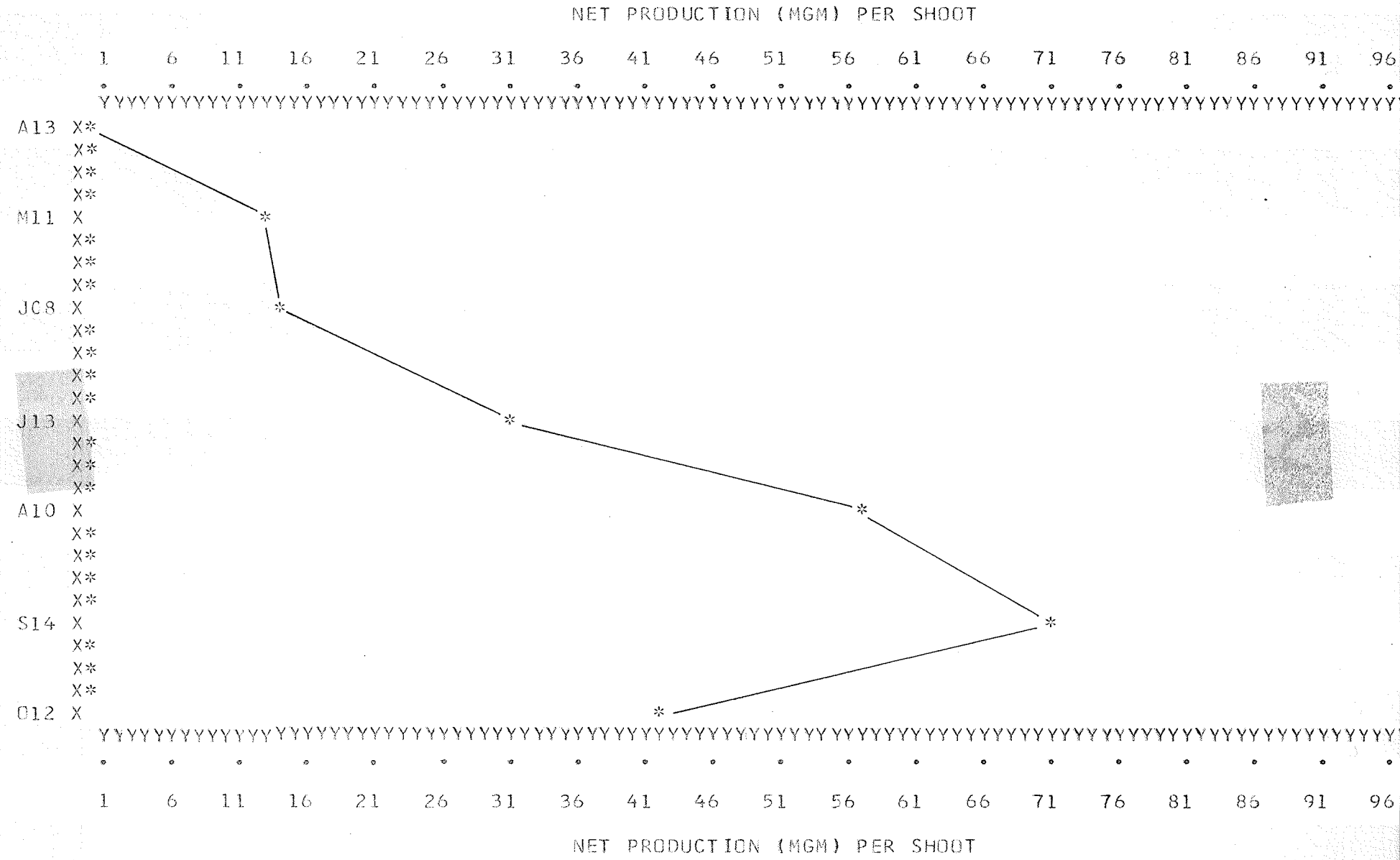

NOTE:PRODUCTION IS 0.04 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:BOG SPECIES:SPHAGNUM FUSCUM PRODUCTION GRAPH



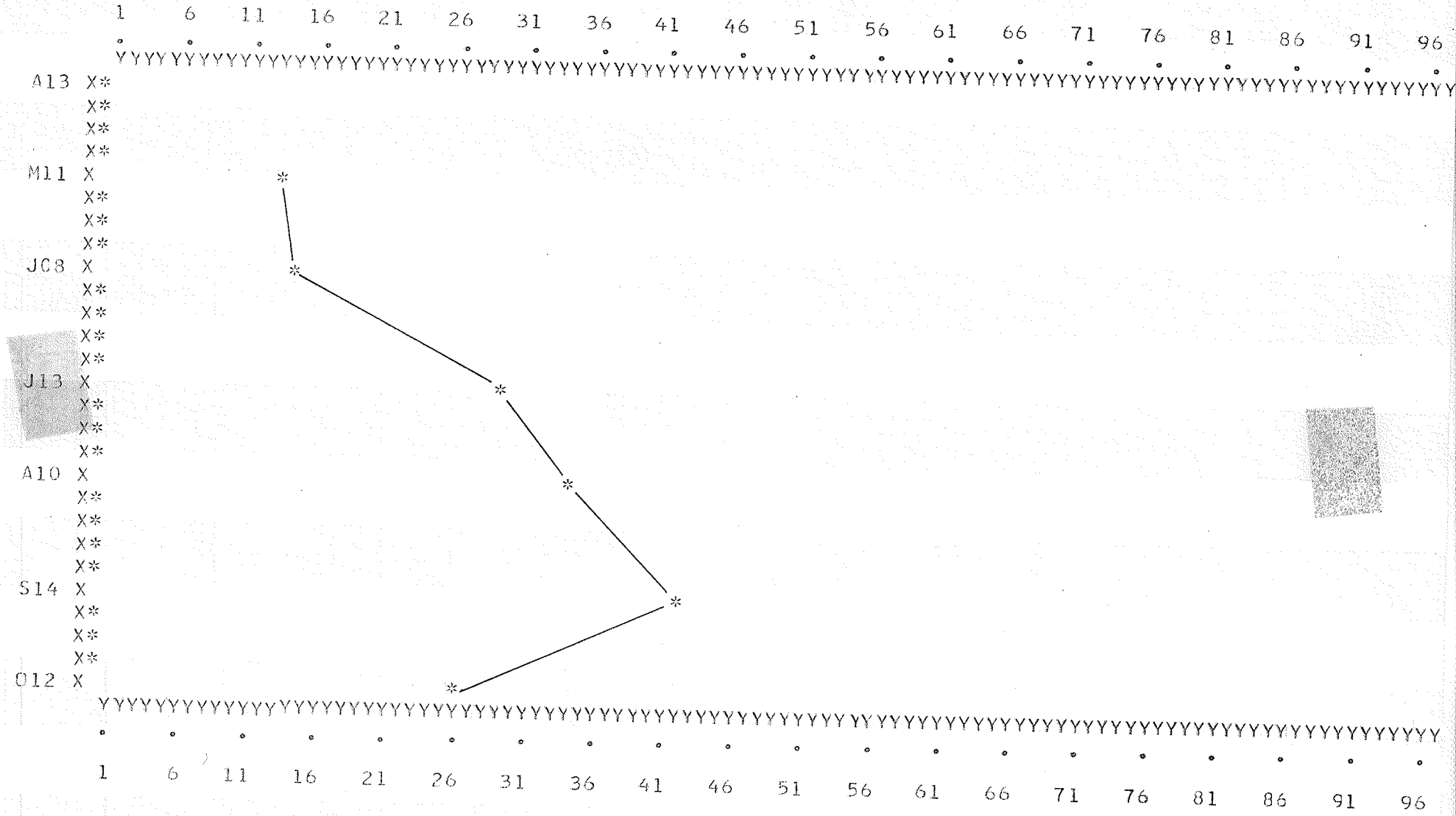

NOTE:PRODUCTION IS 0.01 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:LAGG SPECIES:AULACOMNIUM PALUSTRE PRODUCTION GRAPH




NOTE:PRODUCTION IS 0.03 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:LAGG SPECIES:HYPNUM PRATENSE PRODUCTION GRAPH




NOTE:PRODUCTION IS 0.01 TIMES NUMBER OF Y'S INDICATED ON AXIS

of zonal micro-environments, with one set of environmental conditions being more favourable for growth than the other. Differences were also apparent in production values of Aulacomnium palustre in the Bog and Lagg zones.

Production calculated on an area basis for these species (Table V) was dependent both on the value of individual plant production and on the density of the species in question. While the ranking of the three most productive species was independent of the type of production expression used, i.e., gm./plant or gm./$m.^2$, with Pleurozium schreberi > Polytrichum juniperinum var. gracilius > Aulacomnium palustre (Lagg), the order of importance in the remaining species was changed by expressing production on an area rather than individual basis. For this reason it is preferable to have measures of both individual production and density when comparing species' production. Unfortunately, there are few such values present in the literature.

Longton (1970, p, 829) has observed individual net production in Polytrichum alpestre Hoppe (= P. juniperinum Hedw. var. gracilius Wahlenb.) to be in the range 0.6-3.7 mgm. in various Antarctic locations, compared to the 3.9 mgm. observed in the current study.

With reference to Sphagnum spp., net primary production

TABLE V

MAXIMUM ANNUAL NET PRIMARY PRODUCTION CALCULATED FOR THE IMPORTANT NON-VASCULAR SPECIES FOUND IN EACH OF THE FOUR VEGETATION ZONES

| Zone | Species | (a) Maximum current net primary production per individual mgm. ±1 S.E.%* | (b) Individuals per $cm.^2$ ±1 S.E.% | (c) Cover $cm.^2/m.^2$ ±1 S.E.% | (a)(b)(c) $\sum_{n=1}^{4} Cp_n$ $gm./m.^2$ | Zonal total for important species $gm./m.^2$ |
|---|---|---|---|---|---|---|
| Bog Forest | Pleurozium schreberi | 4.70 ± 6.8% | 2.70 ± 3.7% | 8490 ± 4.6% | 107.7 | 107.7 |
| Muskeg | Sphagnum fuscum | 0.55 ± 5.4% | 4.11 ± 4.6% | 3135 ± 4.1% | 7.1 | 7.1 |
| Bog | Sphagnum fuscum | 0.42 ± 6.9% | 4.11 ± 4.6% | 4515 ± 4.6% | 7.8 | 48.2 |
| | Aulacomnium palustre | 0.49 ± 12.8% | 7.36 ± 5.7% | 1509 ± 2.4% | 5.4 | |
| | Polytrichum juniperinum var. gracilius | 3.94 ± 4.6% | 4.35 ± 9.4% | 2039 ± 2.7% | 35.0 | |
| Lagg | Aulacomnium palustre | 2.13 ± 9.2% | 7.36 ± 5.7% | 2289 ± 3.2% | 35.9 | 67.1 |
| | Hypnum pratense | 0.42 ± 7.3% | 22.75 ± 9.9% | 3260 ± 3.2% | 31.2 | |

* standard error expressed as a percentage

in several species found on a blanket and valley bog in England (Clymo, 1970, p. 34) was at least one order of magnitude larger than values observed in this study. Even when the capitulum weight was added to production values of Sphagnum fuscum the resulting range of biomass values, 39.2-51.8 gm./m.$^2$, (Table VII) was still far below the 269 gm./m.$^2$ determined for the same species by Bellamy and Rieley (1967, p. 39) in England, and the 200-800 gm./m.$^2$ range cited in Overbeck and Happach (1956, p. 363) for locations in northern Europe and Russia. Pearsall & Gorham (1956, p. 198) have suggested that some chlorophyll may be lost by the stems before the end of the growing season, causing production to be underestimated. Since the identification of new growth in the current study was based on the presence or absence of chlorophyll, then this suggests that present results may underestimate annual net production in Sphagnum fuscum.

Pleurozium schreberi, forming a continuous surface layer in the Bog Forest zone, was the most productive of all non-vascular species examined. Its net production value, 107 gm./m.$^2$, was more than twice the 43.5-65.5 gm./m.$^2$ range determined by Weetman (1968, p. 368) for the same species, found under an upland stand of black spruce in eastern Canada.

The wide range of production values exhibited by each of the above species is perhaps attributable to environmental differences between sites examined.

3. Net primary production of other species present

Since not all bryophyte species were considered on an individual basis, then the sum of important species production values in Table V represents an underestimate of the total non-vascular net primary production. Forman (1969, p. 586) has previously made the assumption that unsampled bryophyte species would have a mean biomass value approaching the mean calculated from sampled species. Therefore, zonal net production was estimated by multiplying the sum of important species' production values by the ratio of total/important species' cover percentages (Table VI).

TABLE VI

TOTAL NON-VASCULAR NET PRIMARY PRODUCTION IN EACH OF THE FOUR VEGETATION ZONES

| Zone | (a) Zonal total for important species gm./m.$^2$ | (b) Correction for other species: $\frac{\text{Total cover \% by all species}}{\text{Total cover \% by important species}}$ | (a)(b) NON-VASC. PROD'N gm./m.$^2$ |
|---|---|---|---|
| Bog Forest | 107.7 | 92.5/84.9 | 116.3 |
| Muskeg | 7.1 | 74.9/31.3 | 17.0 |
| Bog | 48.2 | 93.0/80.4 | 55.4 |
| Lagg | 67.1 | 62.9/55.4 | 75.8 |

$$\text{NON-VASC. PROD'N} = \sum_{i=1}^{j} \left( \sum_{n=1}^{4} Cp_n \right) i$$

4. Biomass of non-vascular species

Zonal non-vascular biomass was greater than the corresponding net primary production value, since each of the important species studied had perennial photosynthetic portions. To estimate this biomass, green perennial portions of each species were weighed at each sampling date. This perennial weight, when added to that calculated for net primary production, provided a value for total photosynthetic biomass. Biomass for each of the vegetation zones was then calculated from the sum of species' biomass values, multiplied by the correction factor for unmeasured species (Table VII). This value is likely to underestimate total biomass, as the shoots of certain species may remain alive for a period after losing their chlorophyll (R.E. Longton, personal communication). However, no method was readily available for determining the extent of the brown living portion.

TABLE VII

THE AVERAGE BIOMASS TOTAL FOR NON-VASCULAR SPECIES FOUND IN EACH OF THE FOUR VEGETATION ZONES

| Zone | Species | (a) Mean biomass mgm./individual | (b) Individuals/$m.^2$ | (a)(b) $\sum_{n=1}^{3} Cb_n + \sum_{n=1}^{4} Cp_n$ $gm./m.^2$ | (c) all species cover / Important species cover | (a)(b)(c) Total non-vascular biomass $gm./m.^2$ |
|---|---|---|---|---|---|---|
| Bog Forest | Pleurozium schreberi | 8.08 | 22923 | 185.2 | 1.08 | 200.0 |
| Muskeg | Sphagnum fuscum | 3.04 | 12885 | 39.2 | 2.39 | 93.7 |
| Bog | Sphagnum fuscum | 2.79 | 18557 | 51.8 | 1.15 | 131.3 |
| | Aulacomnium palustre | 1.81 | 11106 | 20.1 | | |
| | Polytrichum juniperinum var. gracilius | 4.77 | 8871 | 42.3 | | |
| Lagg | Aulacomnium palustre | 2.30 | 16849 | 38.8 | 1.13 | 87.5 |
| | Hypnum pratense | 0.52 | 74181 | 38.6 | | |

Total non-vascular biomass = $\sum_{i=1}^{j} [(\sum_{n=1}^{3} Cb_n) + (\sum_{n=1}^{4} Cpn)]_i$

5. The contribution of non-vascular species to accumulation income

As there was little evidence of consumption of bryophytes by herbivores, it was considered that the net primary production of all bryophyte species was added directly to the detritus cycle. The total calculated for non-vascular production represented the annual litter input by these species (Table VIII). In the case of perennial non-vascular species, production was assumed to be of the same order each year. Hence, accumulation income for these species could also be calculated from their current production values.

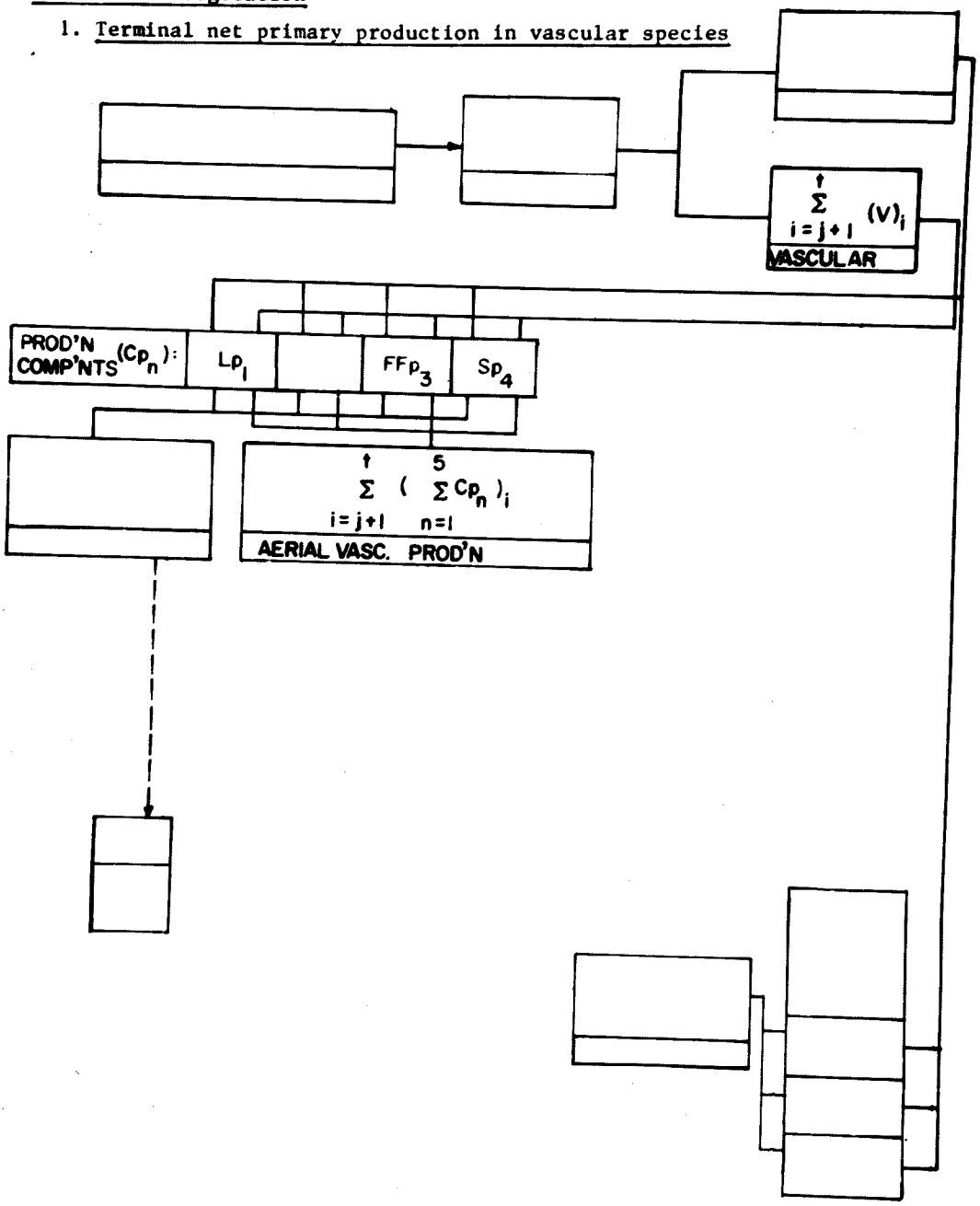
TABLE VIII

THE ANNUAL CONTRIBUTION MADE BY NON-VASCULAR SPECIES TO ACCUMULATION

| Zone | Annual non-vascular litter input gm./m.$^2$ |
|---|---|
| Bog Forest | 116.3 |
| Muskeg | 17.0 |
| Bog | 55.4 |
| Lagg | 75.8 |

D. Biomass, net primary production, and subsequent accumulation of vascular vegetation

1. Terminal net primary production in vascular species



The calculation of net primary production for important vascular species present in each of the four vegetation zones was performed in a manner similar to that previously outlined for non-vascular species. However, in this case, the size of some species, e.g., Picea mariana, led to sampling difficulties. Therefore, important vascular species were divided into two groups (Table IX):

Group "a" - species less than 1.3 meters in height at maturity, where 1.3 meters equals breast height (Newbould, 1967, p. 13).

Group "b" - species equal to, or greater than, 1.3 meters in height at maturity.

This section considers the contribution of new leaves, stems, and flower-fruits, i.e., terminal new growth, to the total production of both group "a" and group "b" species. Also discussed are correction factors which estimate production lost as litter during the growing season.

(a) Sampling scheme for group "a" species

Sampling involved the weekly clipping of a minimum of 80 terminal growing points from each of the important vascular species being considered. These were taken from the 25x25 cm. quadrats described previously. Since more than one quadrat was harvested at each sampling date, subsequent areas sampled at each of

TABLE IX

IMPORTANT VASCULAR SPECIES

| Important species | Bog Forest | Muskeg | Bog | Lagg |
|---|---|---|---|---|
| Group "a" species: | | | | |
| *Ledum groenlandicum* | + | + | + | |
| *Chamaedaphne calyculata* | | + | + | + |
| *Vaccinium vitis-idaea* var. *minus* | | + | + | |
| *Kalmia polifolia* | | + | + | |
| *Oxycoccus quadripetalus* | | | + | |
| *Carex rostrata* | | | | + |
| *Calamagrostis canadensis* | | | | + |
| Group "b" species: | | | | |
| *Picea mariana* | + | + | | |
| *Salix bebbiana* | | | | + |
| *Salix serissima* | | | | + |

the eight positions extended along a straight line perpendicular to the length (N-S) of the study plot. It was expected that variation in species composition could be minimized by following this sampling procedure.

Buffer areas, 25x25 cm. in size, were left between sampled quadrats, since experience indicated that sampling had a destructive influence on the bryophyte component of adjacent unsampled quadrats.

Collected material was placed in polyethylene bags, one bag per 25x25 cm. area, and returned to the laboratory. Here the contents of each bag were separated into species and components. This separated material was ovendried at 105°C. to constant weight, cooled in closed polyethylene bags, and weighed.

By counting the number of terminal portions employed in the sample mean production per growing point was calculated for each species analyzed. To determine a species' net production on an area basis, the number of growing points found in quadrats sampled throughout the growing season was recorded and an average density value for each species calculated. These density values were multiplied by production/growing point values to provide an estimate of terminal new growth on an area basis.

(b) Sampling scheme for group "b" species

This group is composed of species which at maturity have

a height equal to, or greater than, breast height.

According to relative frequency values, only Salix bebbiana, Salix serissima, and Picea mariana required individual sampling. However, due to their size it was found impossible to sample these species on a quadrat basis. Instead, at each sampling date a total of eighty terminal new growth portions, consisting of new leaves, stems, and reproductive structures, were clipped from trees of average zonal circumference in the case of P. mariana, and of average zonal height for each of the Salix species. Whenever possible, terminal portions were clipped from a single tree.

These clipped terminal portions were placed in polyethylene bags and taken back to the laboratory, where they were separated into leaf, stem, and flower-fruit, dried at 105°C., cooled in a desiccator, and finally weighed.

Knowing the number of terminal portions employed in the sample allowed a value of net production per growing point to be calculated for each of the components. To calculate net primary production on an area basis, density was estimated for each species as the product of the number of terminal growing points per rooted stem, and the number of rooted stems per square meter. For P. mariana, an estimate of the number of rooted stems per square meter was obtained using the quarter method (Cottam and

Curtis, 1956). The circumference of trees encountered was also measured, from which the average tree circumference was determined. A tree having this circumference was selected and the total number of individuals on this rooted stem were counted.

Density for Salix spp. was determined by counting the number of rooted stems in sixteen 5x5 meter quadrats. These quadrats were located at five meter intervals along the transect used to determine cover values in the Lagg zone. The height of the first twenty trees of S. bebbiana and S. serissima was measured and an average height calculated for each species. Trees of this average height were examined, and the number of individuals present was recorded. The product of the number of individuals per rooted stem and the number of rooted stems per square meter was multiplied by individual production values to provide an estimate of terminal net primary production on an area basis.

(c) Correction factors for litter lost from terminal portions

Values of terminal production had to be corrected for the loss of leaves and flower-fruits, since not all of the dry matter produced in the current growing season remained attached to living portions.

Mesh bags (Figure 14) were employed in all four zones to enclose a number of individuals of each important species. In

Figure 14. Bag-types employed in determining litter correction factors.

(a) Cheesecloth bag used to partially enclose large individuals, e.g., Chamaedaphne calyculata (May, 1970). Marker pole colour band = 20 cm.

(b) Nylon bag used to partially enclose smaller individuals, e.g., Picea mariana (July, 1970).

each of these bags both the number of attached new leaves and the number of visible leaf scars were counted at each sampling date. By equating the weight of leaves harvested with the number of attached leaves found in a litter bag at that same date, both the weight of leaves lost through death and the total corrected production could be calculated as in the following example:

Total weight of new leaves of species V harvested per zone = 5.00 gm.

Number of new standing leaves of species V in two litter bags in that same zone = 13

Number of fallen new leaves of species V in two litter bags in that same zone = 2

Then assuming 13 leaves = 5.00 gm.

Total production is 13 + 2 = 15 leaves having a weight of $\frac{15}{13} \times 5.00 = 5.77$ gm.

This correction method was applied to leaf data gathered at each sampling date during the growing season. While leaves lost as litter could be expected to weigh less than others remaining attached for longer periods of time, all leaves were assumed to be equal in weight when applying the correction factor. Since the observed leaf weight was never corrected by more than ten percent for any species, except Salix bebbiana

(0% - 25%), then the error in making this assumption was not critical.

To calculate the amount of current production lost by reproductive structures during the growing season the number of visible flower-fruit scars was counted at each sampling date. Flower weight losses could not be made according to the above example for leaves, since only corollas and stamens were lost early in the growing season. Therefore, the ratio of corolla to total flower weight was determined for several of the important ericoids; namely, Ledum groenlandicum, Kalmia polifolia, Vaccinium vitis-idaea var. minus, and Oxycoccus quadripetalus. The average value was 0.293 ± 11.7%.

The observed flower weight was corrected by adding to it the value of the following expression:

$$\frac{\text{number of new corollas lost per litter bag}}{\text{number of standing new corollas per litter bag}} \times \text{(harvested weight of new flowers)} \times (0.293)$$

Later in the season, when flower-fruit counts indicated that mature fruits were falling, the leaf correction method was employed to correct flower-fruit production totals.

It is these corrected values for leaf and flower-fruit production which appear in Table X.

(d) Terminal component net primary production values

When the weekly sums of terminal component production

were examined graphically (Programme 2), a sigmoid growth curve could be traced in most cases. The two herbaceous species, Carex rostrata and Calamagrostis canadensis, proved to be exceptions, with a linear relationship between time and growth evident.

In several cases, e.g., Kalmia polifolia in the Muskeg zone, there was considerable weekly fluctuation in the production values forming the upper plateau of the logistic curve. Such fluctuation is in part a result of natural variation among individual plants in the populations sampled. This fluctuation could be minimized by either measuring the same plants throughout the growing season, or by increasing the number of plants harvested at each date.

The maximum production value for each of the terminal components was recorded in Table X. By combining these production values with density values recorded in Table XI, values of net primary production per unit area were obtained for each of the important vascular species studied (Table XII).

In general, Tables X and XII indicate that the greatest proportion of total production was present in the leaves, followed by reproductive structures, and finally terminal stems. The proportion of production chanelled into flowers and fruits was unusually large, especially in the ericoid species, where,

with the exception of Ledum groenlandicum, the weight of reproductive structures was up to one half the weight calculated for leaves of the same species.

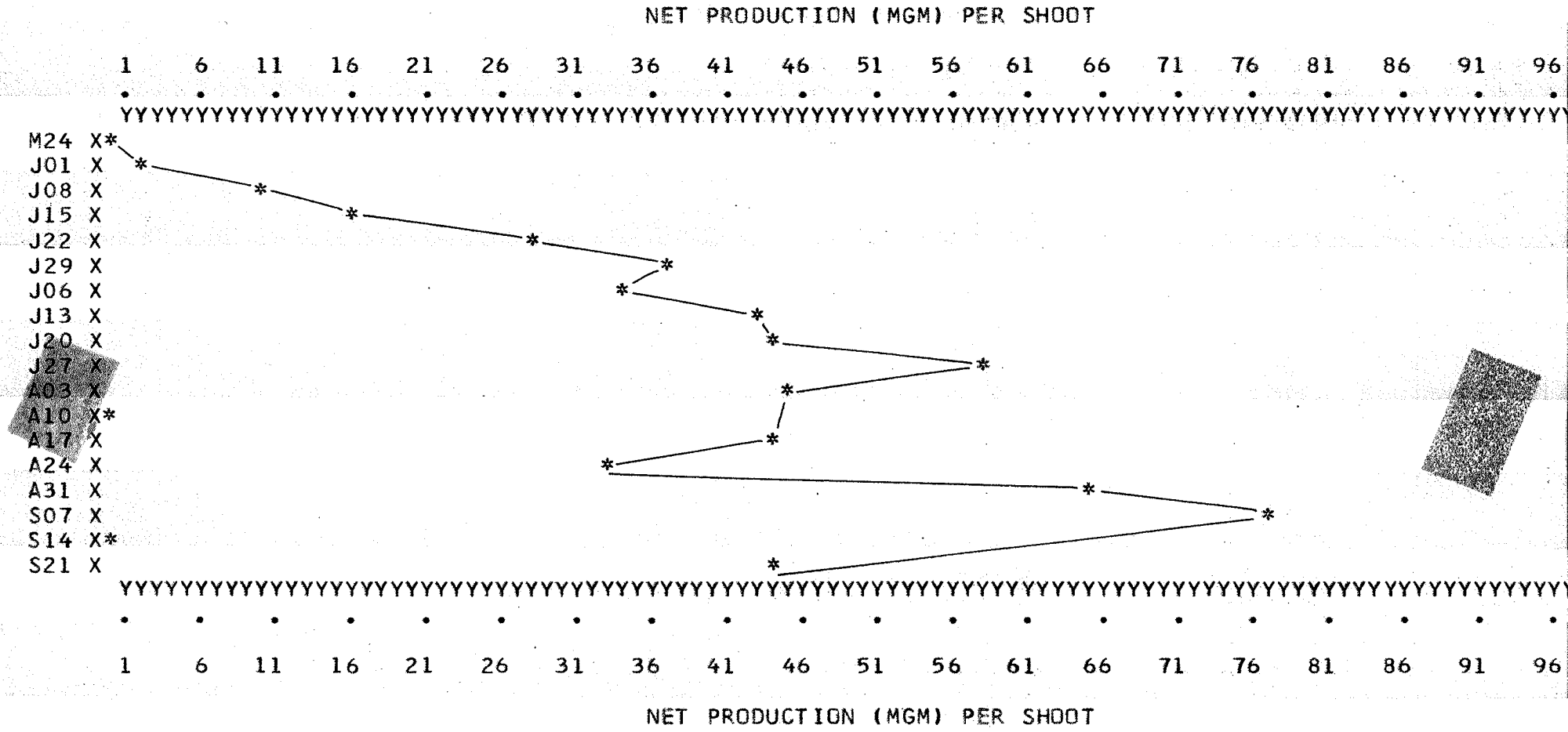
Differences in the production and density values of species found in more than one zone again suggested that there were microenvironmental differences among the zones.

Programme 2. Terminal component net production, i.e., new leaf plus new stem plus new flower-fruit, observed in individuals of each of the important vascular species studied during the 1970 growing season.

```
C PROGRAMME 2
C------------
C
C THIS PROGRAMME,WRITTEN IN WATFIV,GRAPHICALLY PRESENTS
C THE PATTERN OF WEIGHT INCREMENT IN INDIVIDUALS
C OF EACH OF THE IMPORTANT VASCULAR SPECIES STUDIED
C
C SOURCE PROGRAMME LISTING
C-------------------------
C
      DIMENSION XLINE(100),IC2(18),LINE(100),YLINE(100)
      CHARACTER*10 $ZONE(21)
      CHARACTER*35 $SPEC(21)
      CHARACTER $P*4(8),$DATE*3(18)
      DATA $P/'NET ','PROD','UCTI','ON (','MGM)',' PER',' SHO','OT  '/
      DATA $DATE/'M24','J01','J08','J15','J22','J29','J06','J13','J20',
     *'J27','A03','A10','A17','A24','A31','S07','S14','S21'/
      DATA YAX/'Y'/,STAR/'*'/,BLANK/' '/,XAX/'X'/
      DATA $PER/'.'/
      N=21
      DO 9000 I = 1,N
      READ(5,6000) $ZONE(I),$SPEC(I)
 6000 FORMAT(A10,A35)
      READ(5,1600) (IC2(IT),IT=1,18),SCALE
 1600 FORMAT(18I3,F5.1)
 1141 WRITE(6,5000) $ZONE(I),$SPEC(I)
 5000 FORMAT('1',' ZONE:',A10,' SPECIES:',A35,' PRODUCTION GRAPH ')
      WRITE(6,100) $P
  100 FORMAT('0',45X,8A4)
      DO 222 L=1,100,5
      LINE(L) = L
      YLINE(L) = $PER
  222 CONTINUE
       WRITE(6,121) (LINE(L),L=1,100,5)
  121 FORMAT('0',9X,20(I2,3X))
      WRITE(6,787) (YLINE(L),L=1,100,5)
  787 FORMAT(' ',9X,20(1X,A1,3X))
      DO 200 IP = 2,100,1
      XLINE(1) = BLANK
  200 XLINE(IP) = YAX
      WRITE(6,300) XLINE
  300 FORMAT(' ',9X,100A1)
      DO 400 IP = 1,100,1
  400 XLINE(IP) = BLANK
      KP = 18
      DO 700 JP = 1,KP
      XLINE(1) = XAX
      IP = IC2(JP) + 2
      XLINE(IP) = STAR
      WRITE(6,500) $DATE(JP),XLINE
  500 FORMAT(' ',4X,A3,1X,100A1)
      XLINE(IP) = BLANK
  700 CONTINUE
      DO 600 IP = 2,100,1
      XLINE(1) = BLANK
  600 XLINE(IP) = YAX
      WRITE(6,7000) XLINE
```

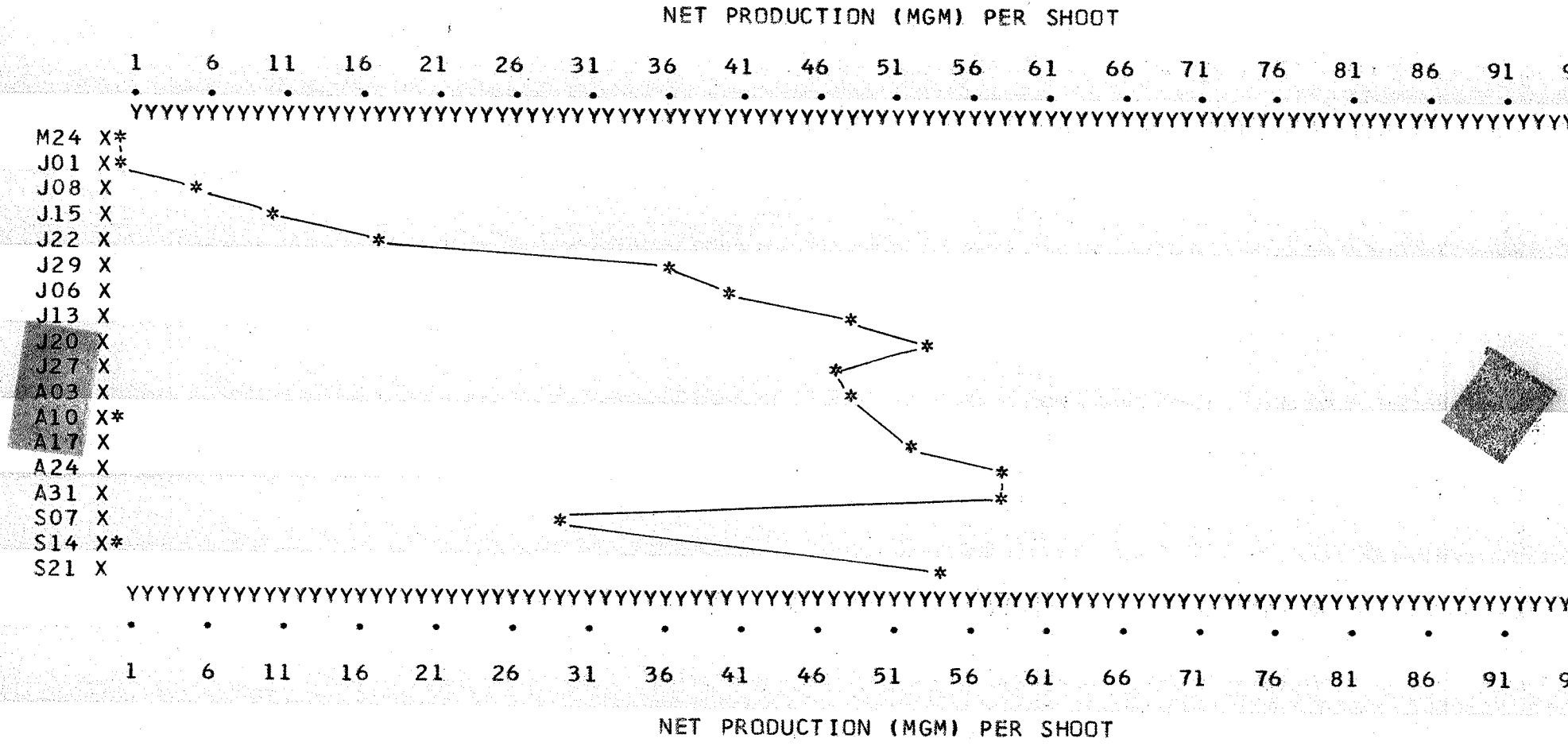
```
7000 FORMAT(' ',9X,100A1)
     DO 333 LL = 1,100,5
     LINE(LL) = LL
     YLINE(LL) = $PER
 333 CONTINUE
     WRITE(6,787) (YLINE(LL),LL=1,100,5)
     WRITE(6,121) (LINE(LL),LL=1,100,5)
     WRITE(6,800) $P
 800 FORMAT('0',45X,8A4)
 900 WRITE(6,1000) SCALE
1000 FORMAT('-','NOTE:PRODUCTION IS ',F5.1,
    *' TIMES NUMBER OF Y''S INDICATED ON AXIS ')
9000 CONTINUE
     STOP
     END
```

ZONE:BOG FOREST SPECIES:PICEA MARIANA PRODUCTION GRAPH



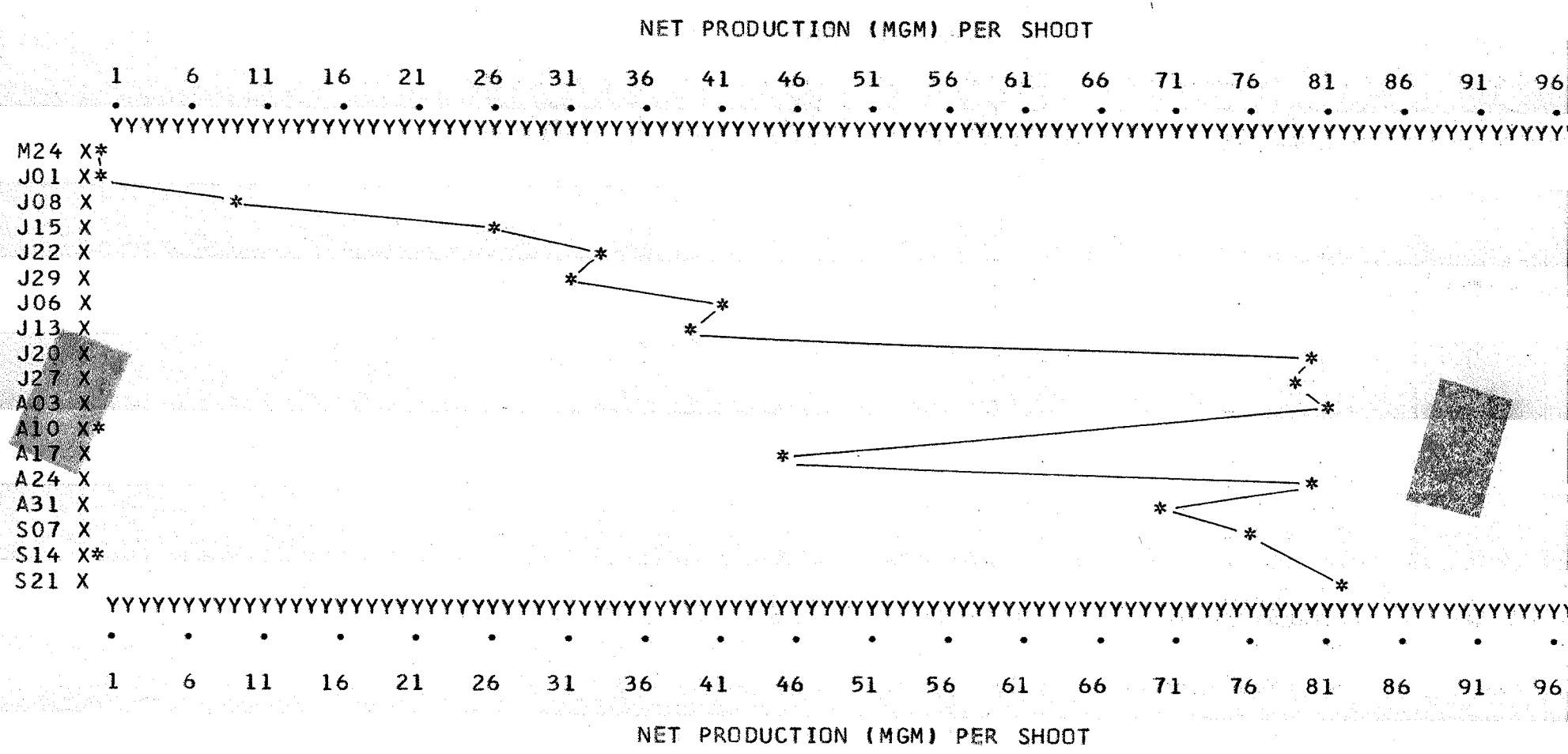

NOTE:PRODUCTION IS 2.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:BOG FOREST SPECIES:LEDUM GROENLANDICUM PRODUCTION GRAPH



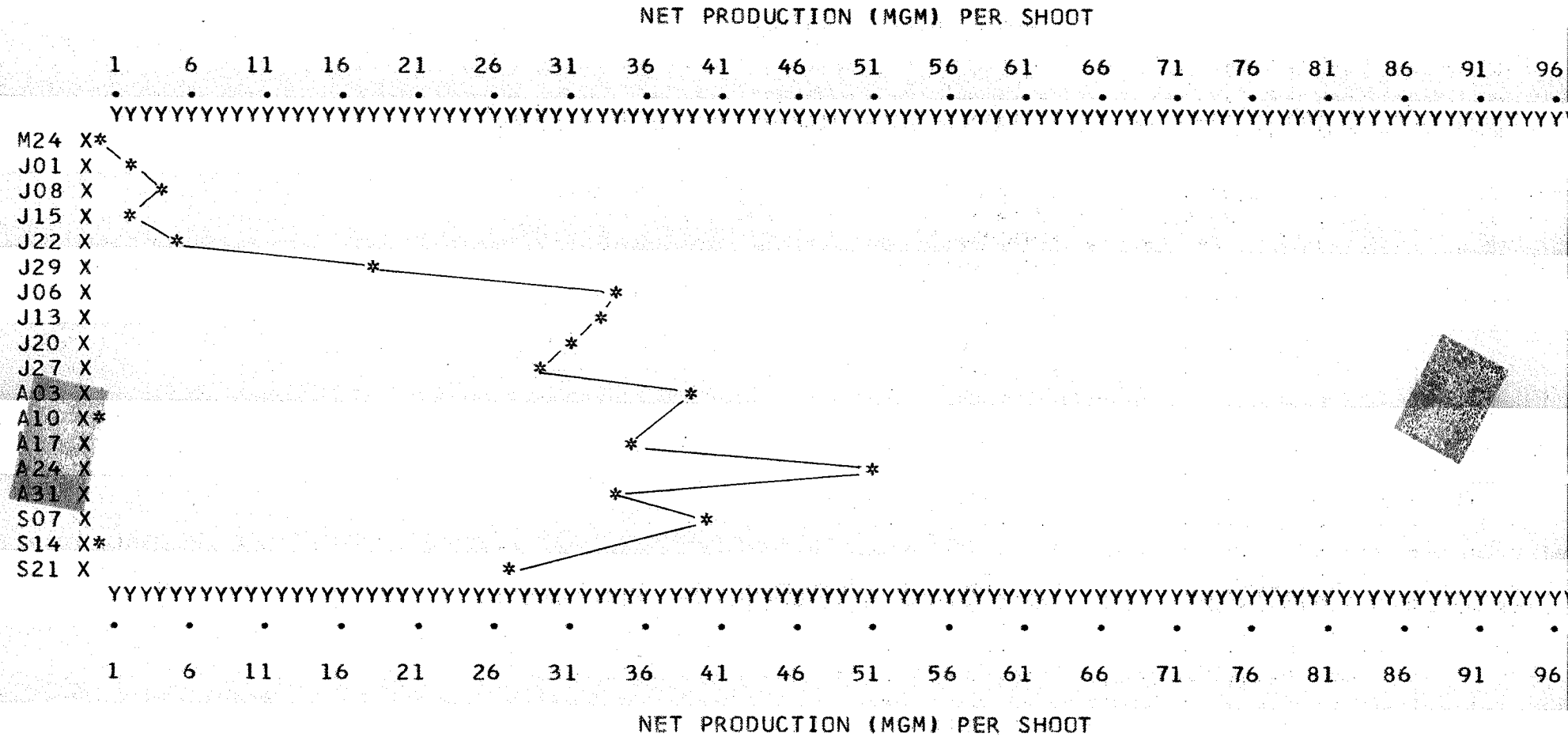

NOTE:PRODUCTION IS 1.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:MUSKEG SPECIES:PICEA MARIANA PRODUCTION GRAPH



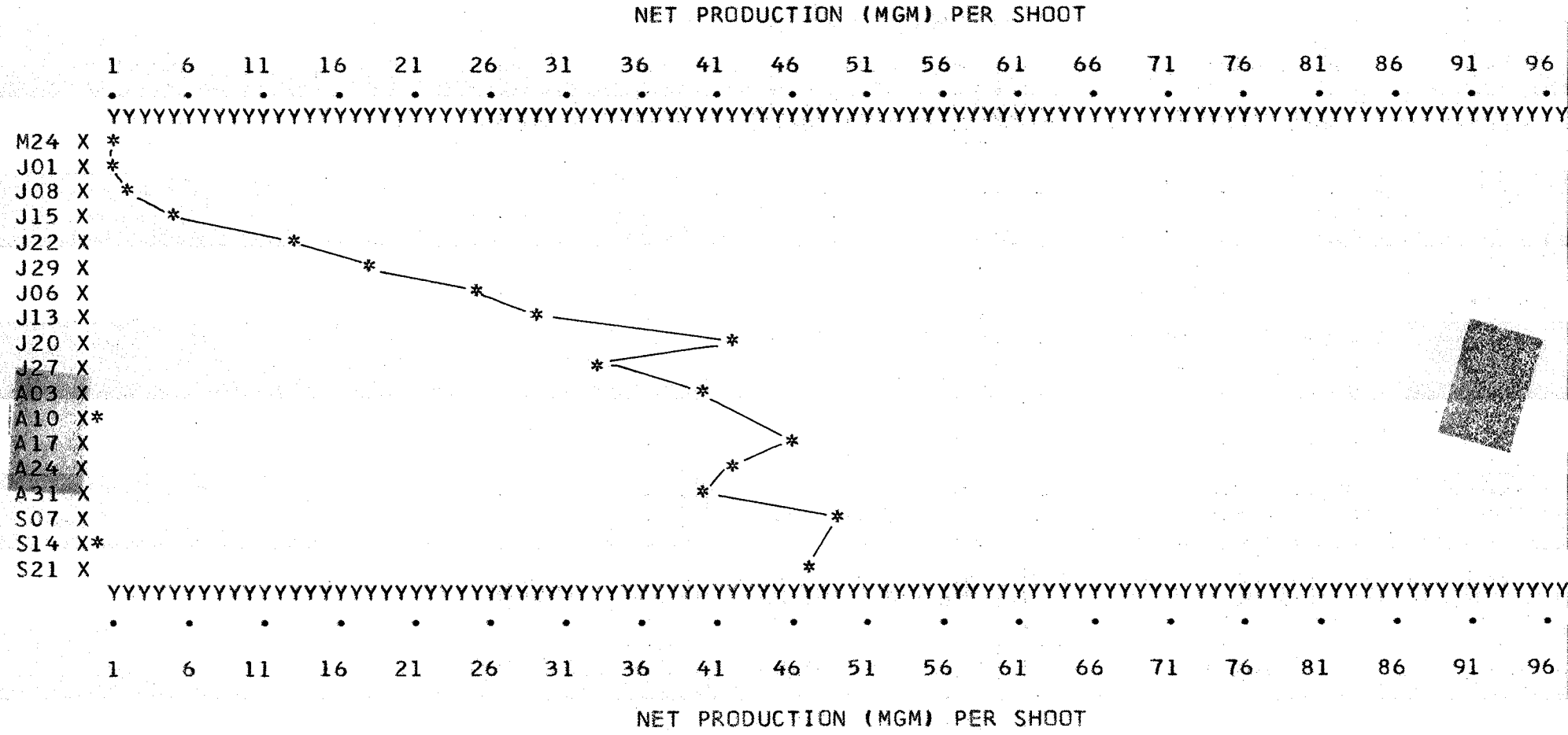

NOTE:PRODUCTION IS 1.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:MUSKEG SPECIES:LEDUM GROENLANDICUM PRODUCTION GRAPH



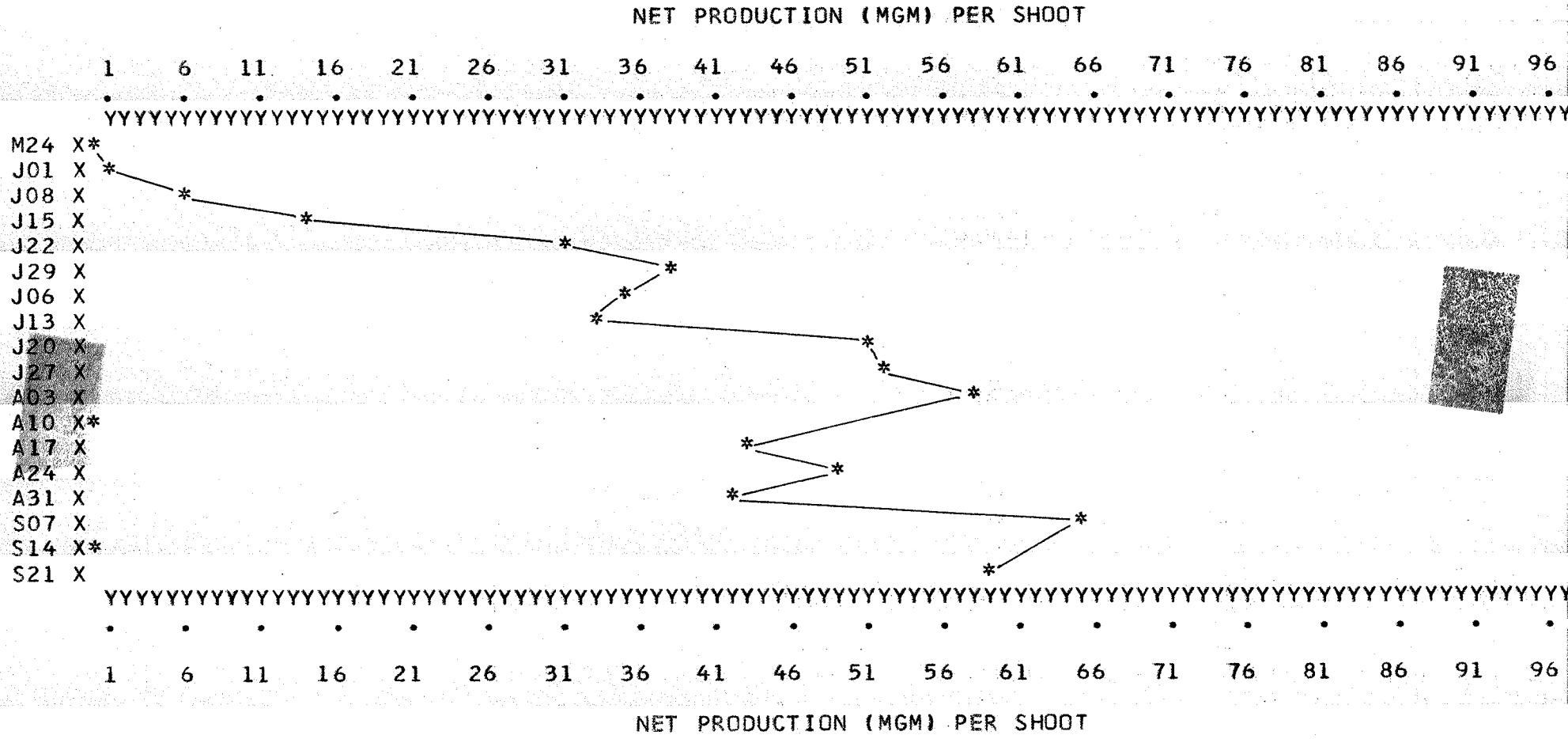

NOTE:PRODUCTION IS 2.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:MUSKEG SPECIES:CHAMAEDAPHNE CALYCULATA PRODUCTION GRAPH



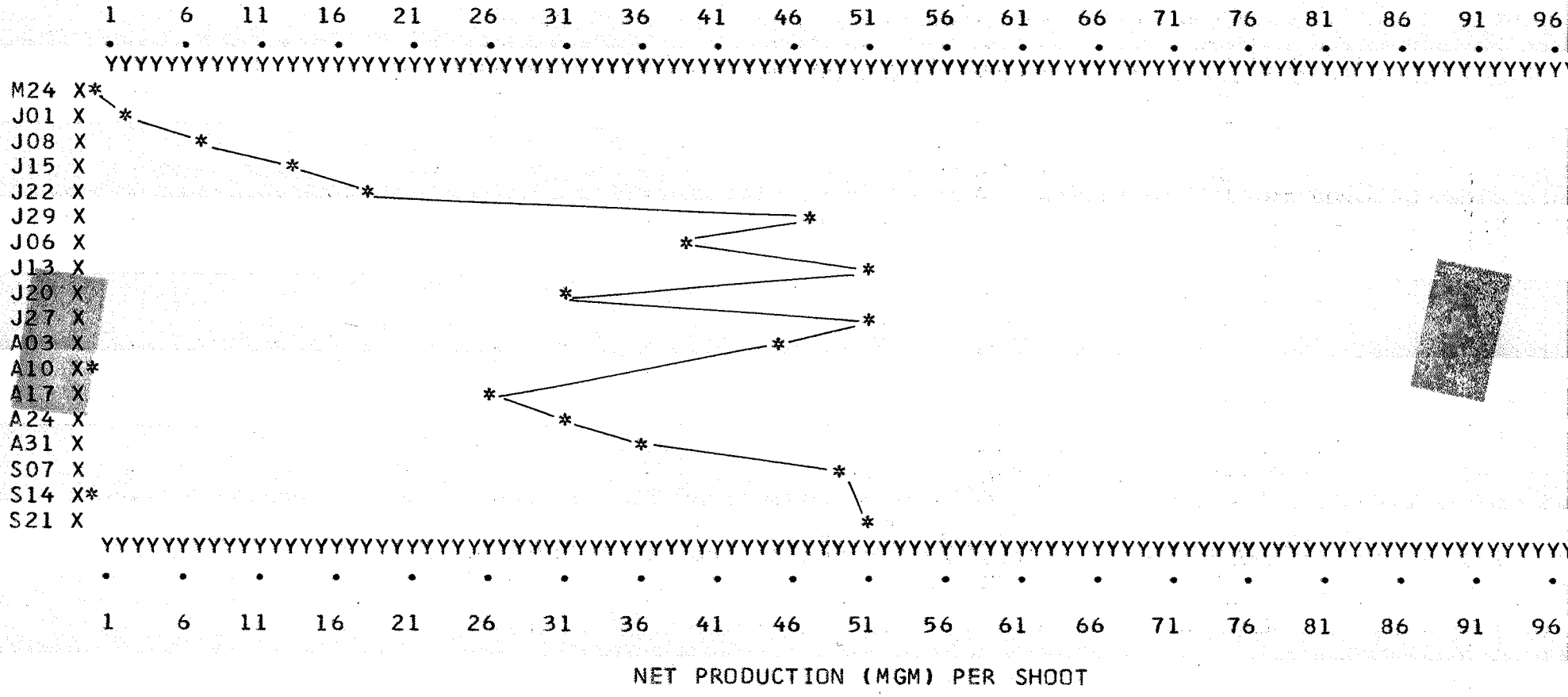

NOTE:PRODUCTION IS 2.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:MUSKEG SPECIES:VACCINIUM VITIS-IDAEA VAR. MINUS PRODUCTION GRAPH



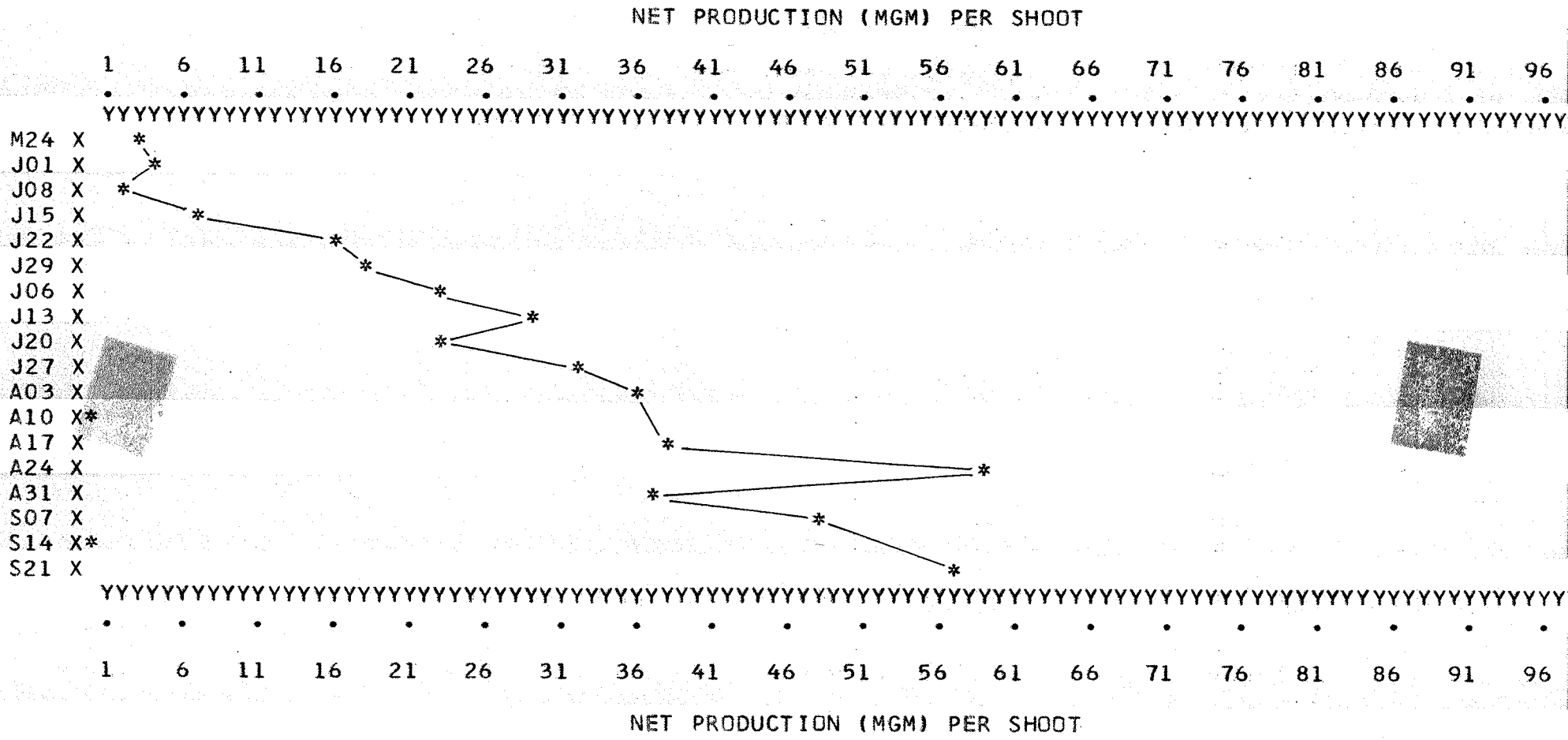

NOTE:PRODUCTION IS 1.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:MUSKEG SPECIES:KALMIA POLIFOLIA PRODUCTION GRAPH



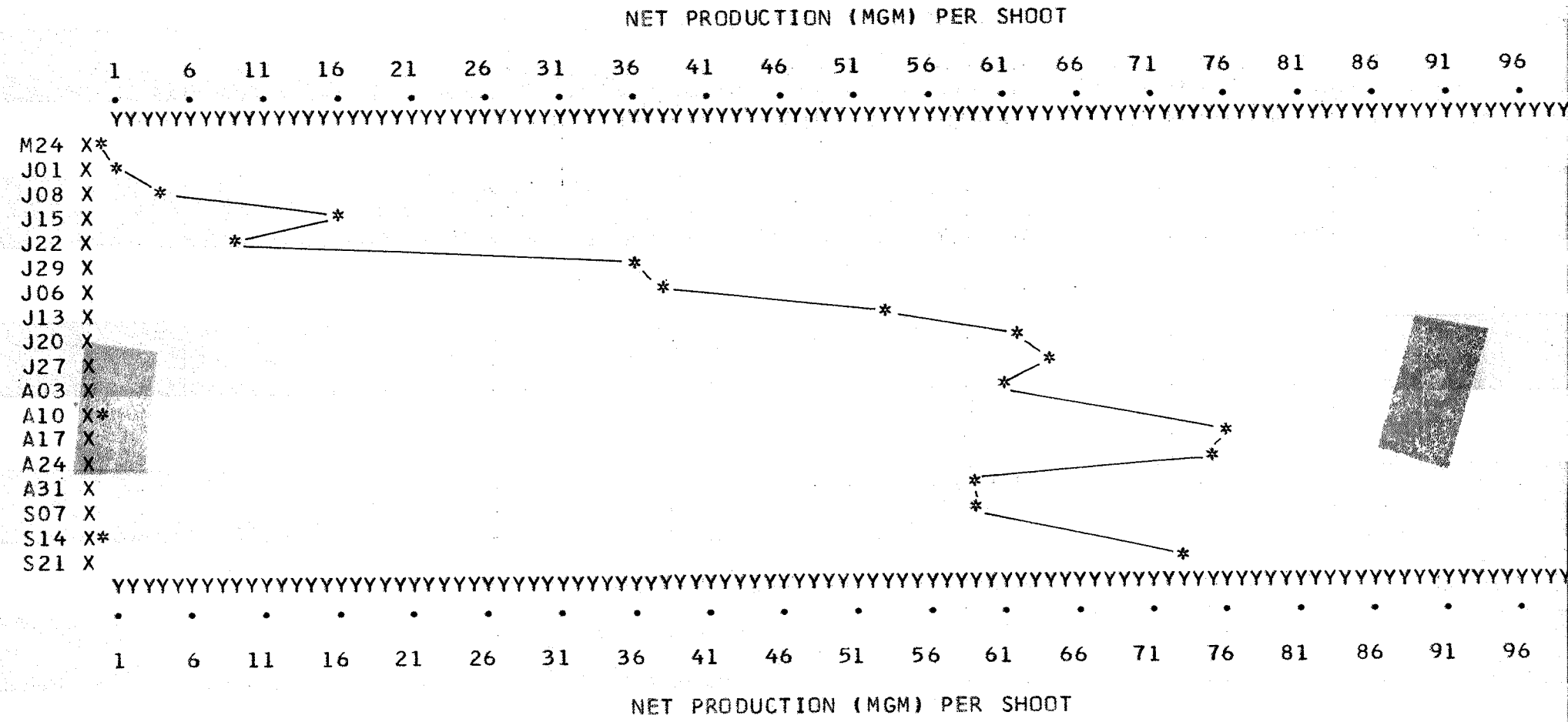

NOTE:PRODUCTION IS 1.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:BOG SPECIES:CHAMAEDAPHNE CALYCULATA PRODUCTION GRAPH



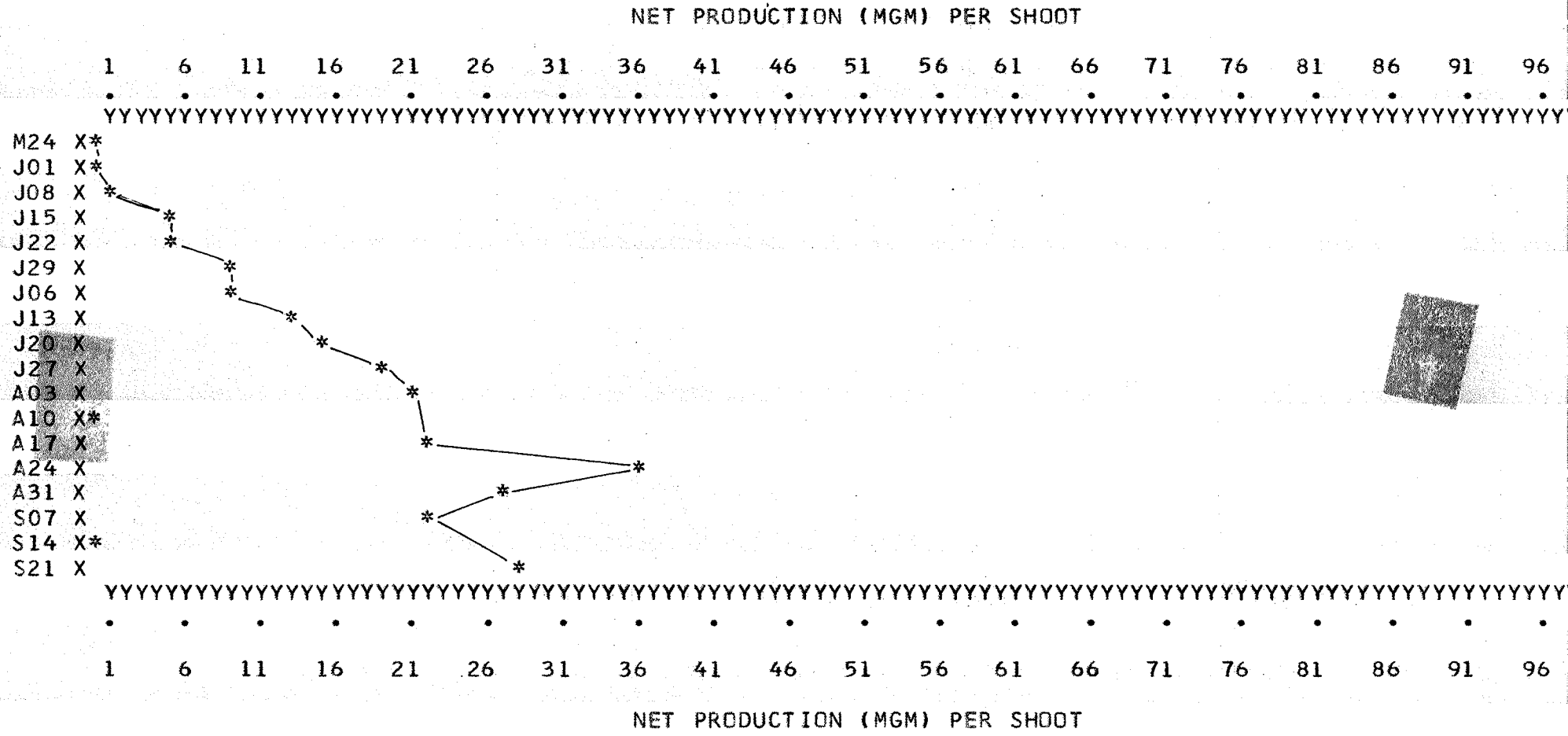

NOTE:PRODUCTION IS 2.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:BOG SPECIES:LEDUM GROENLANDICUM PRODUCTION GRAPH



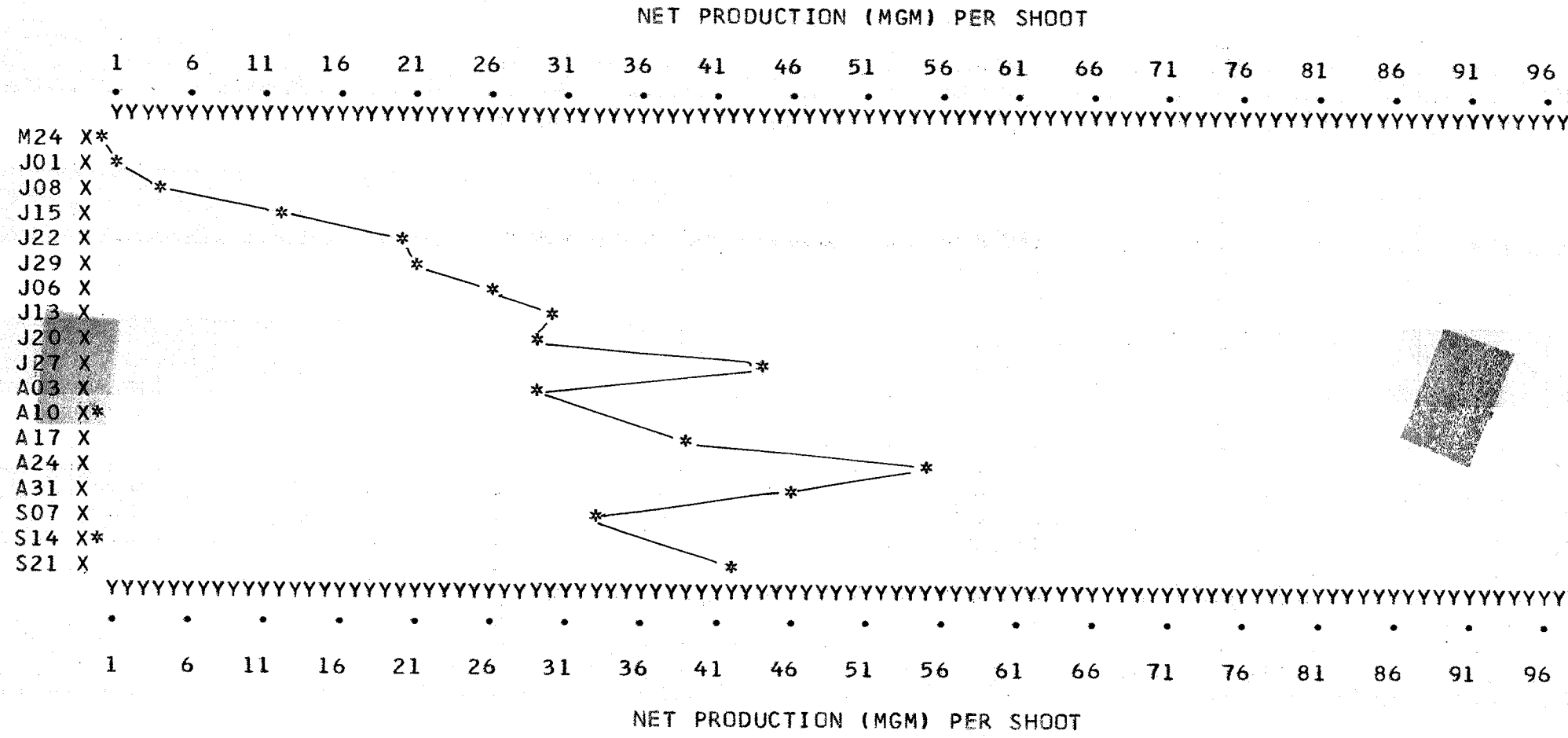

NOTE:PRODUCTION IS 1.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:BOG SPECIES:OXYCOCCUS QUADRIPETALUS PRODUCTION GRAPH




NOTE:PRODUCTION IS 1.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

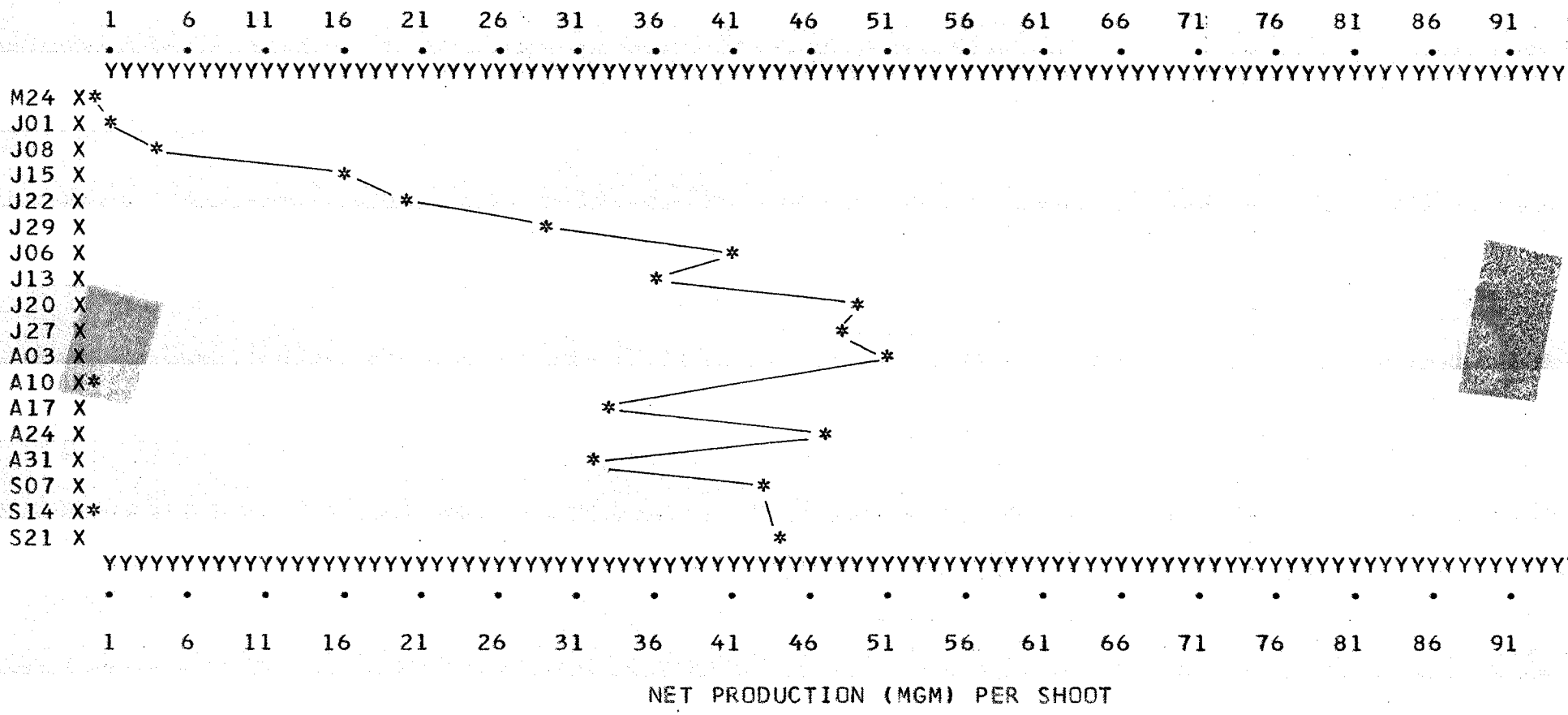
ZONE:BOG SPECIES:VACCINIUM VITIS-IDAEA VAR. MINUS PRODUCTION GRAPH




NOTE:PRODUCTION IS 1.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:BOG SPECIES:KALMIA POLIFOLIA PRODUCTION GRAPH

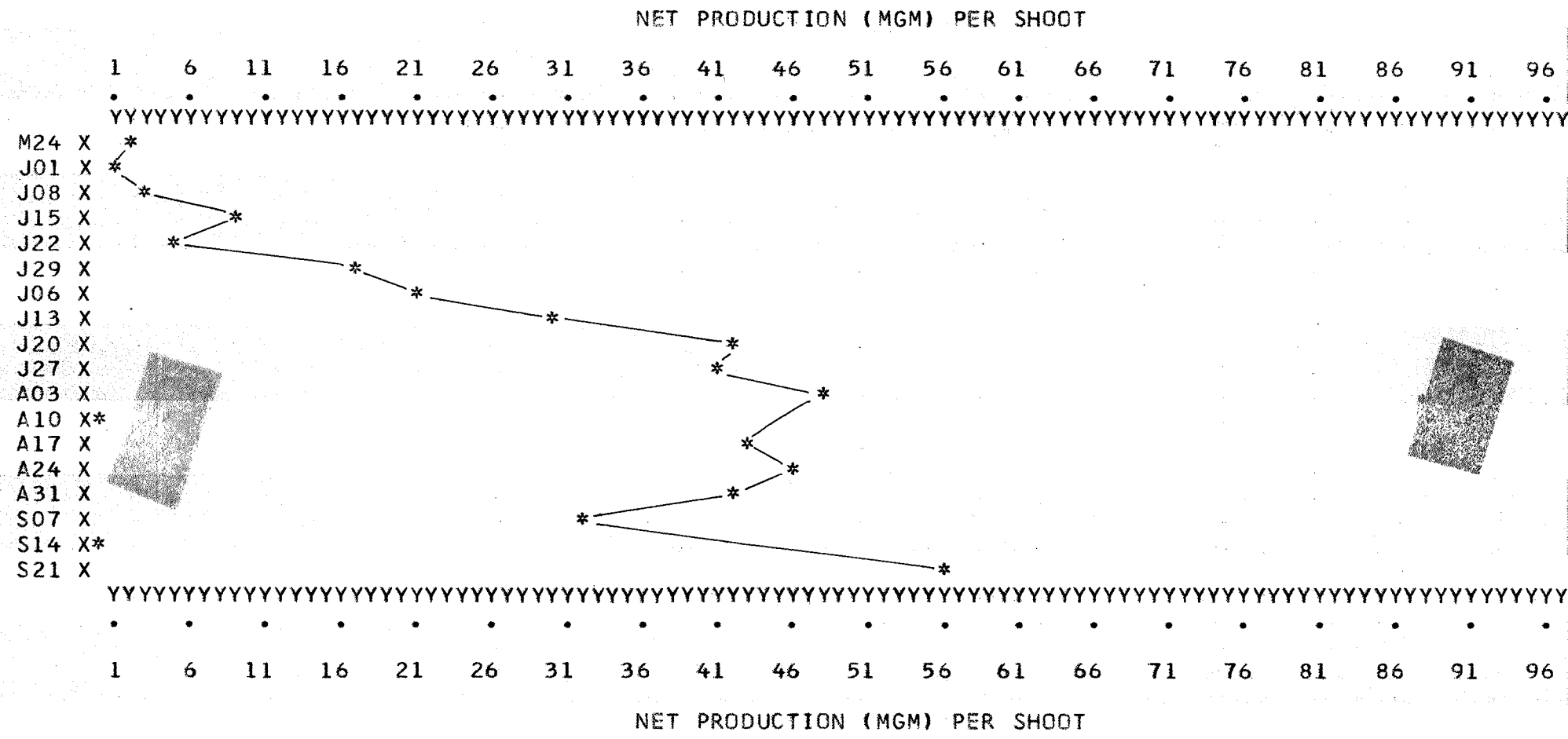
NET PRODUCTION (MGM) PER SHOOT




NET PRODUCTION (MGM) PER SHOOT

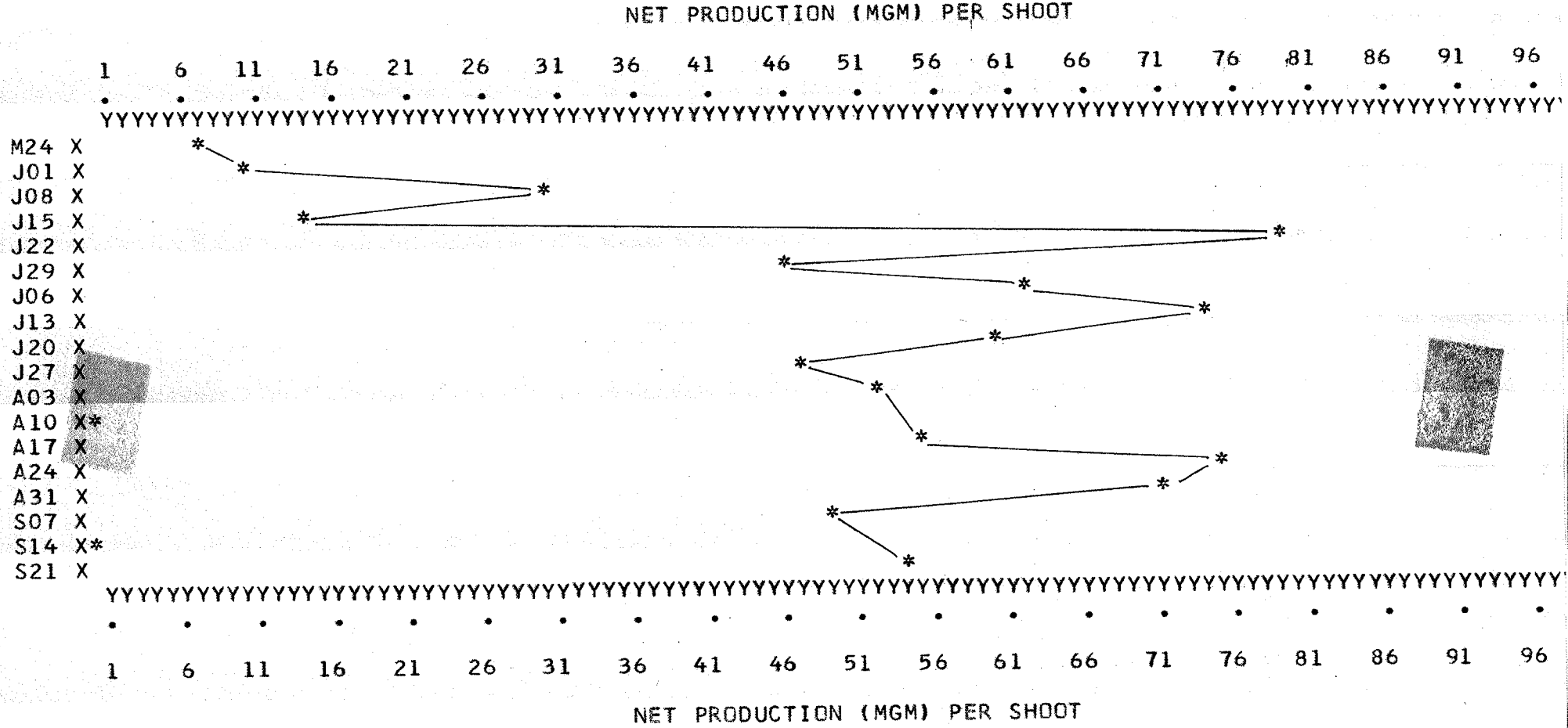
NOTE:PRODUCTION IS 1.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:LAGG SPECIES:CHAMAEDAPHNE CALYCULATA PRODUCTION GRAPH



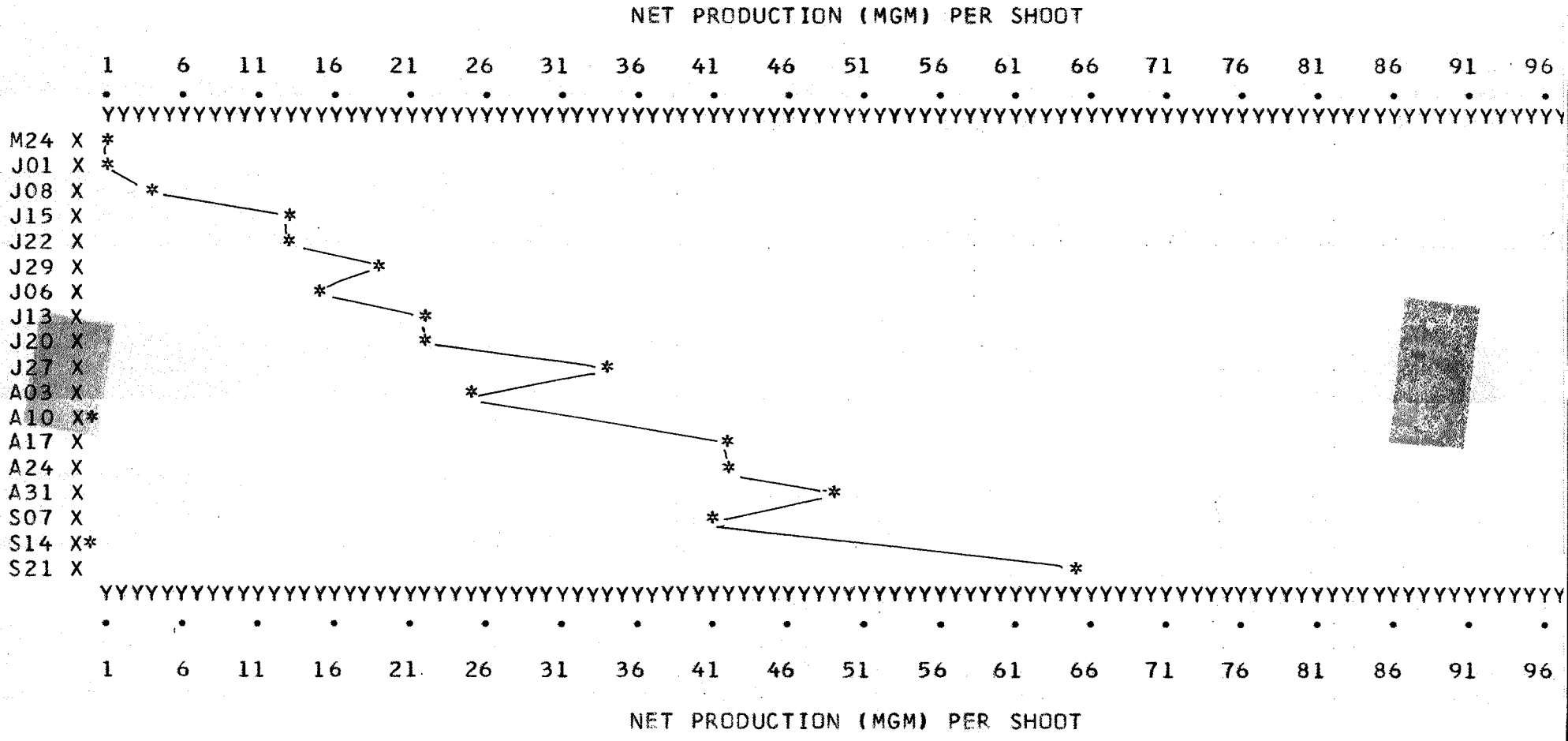

NOTE:PRODUCTION IS 2.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:LAGG SPECIES:SALIX BEBBIANA PRODUCTION GRAPH



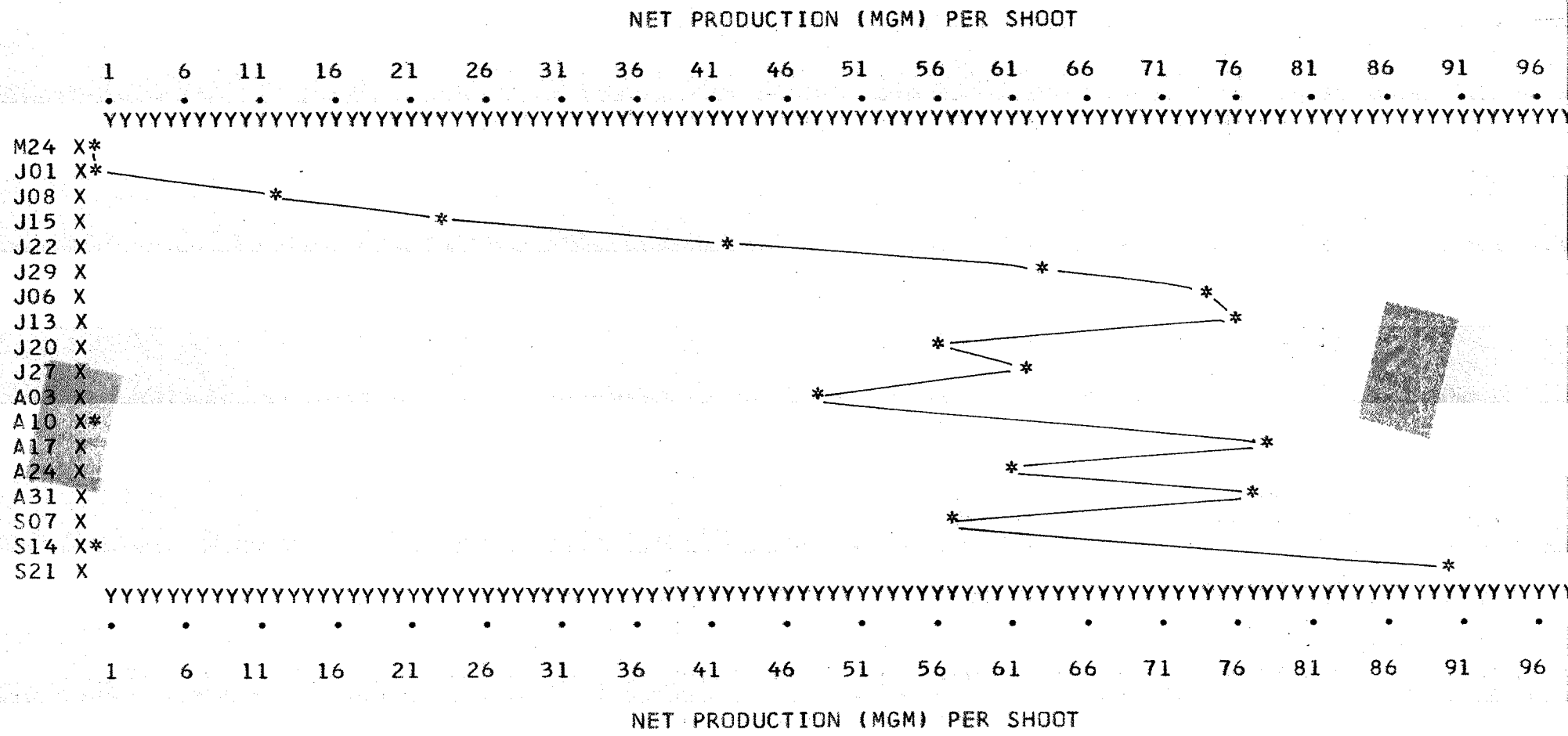

NOTE:PRODUCTION IS 2.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:LAGG SPECIES:CAREX ROSTRATA PRODUCTION GRAPH



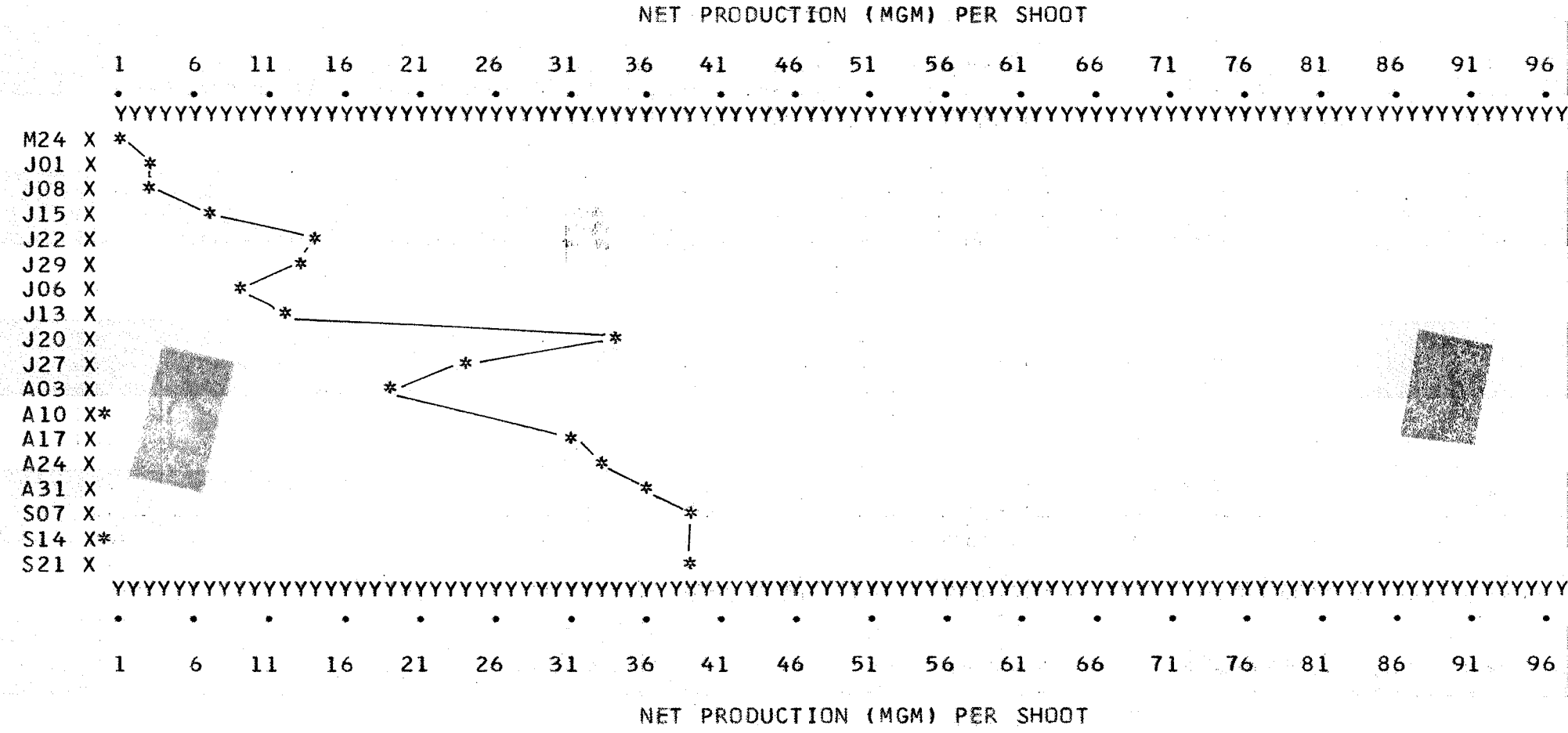

NOTE:PRODUCTION IS 50.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:LAGG SPECIES:SALIX SERISSIMA PRODUCTION GRAPH




NOTE:PRODUCTION IS 3.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

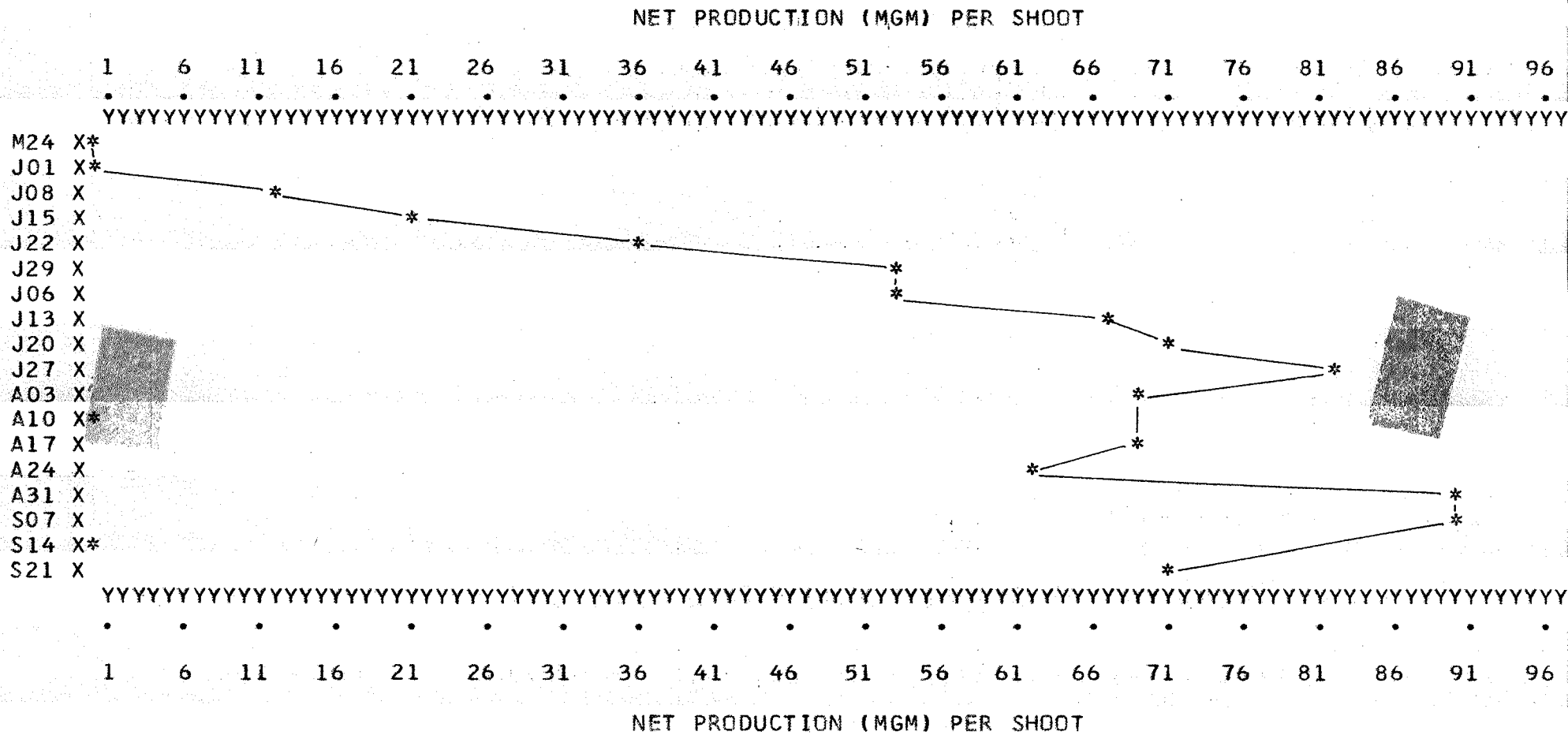
ZONE:LAGG SPECIES:CALAMAGROSTIS CANADENSIS PRODUCTION GRAPH




NOTE:PRODUCTION IS 10.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

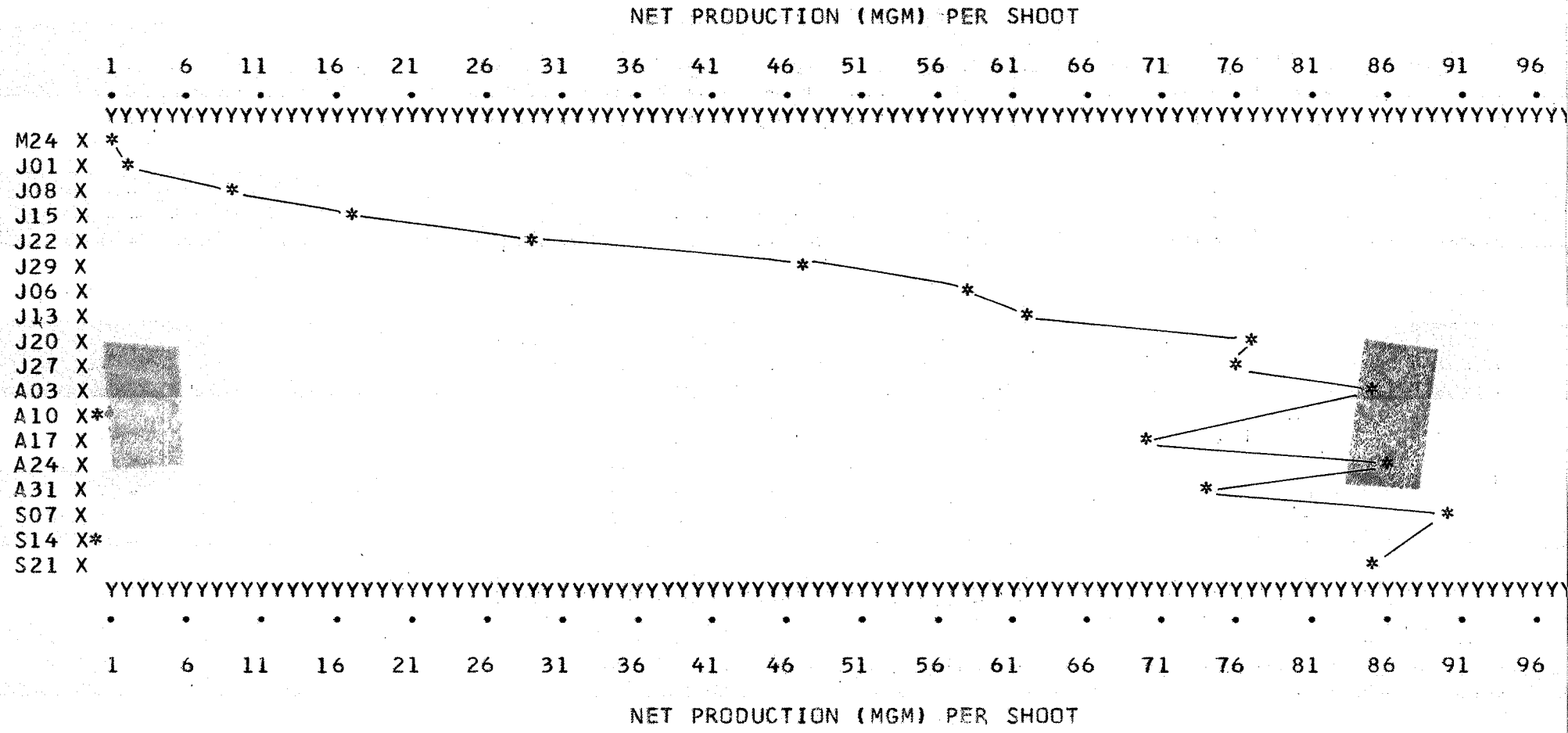
ZONE:BOG FOREST SPECIES:ALL

PRODUCTION GRAPH



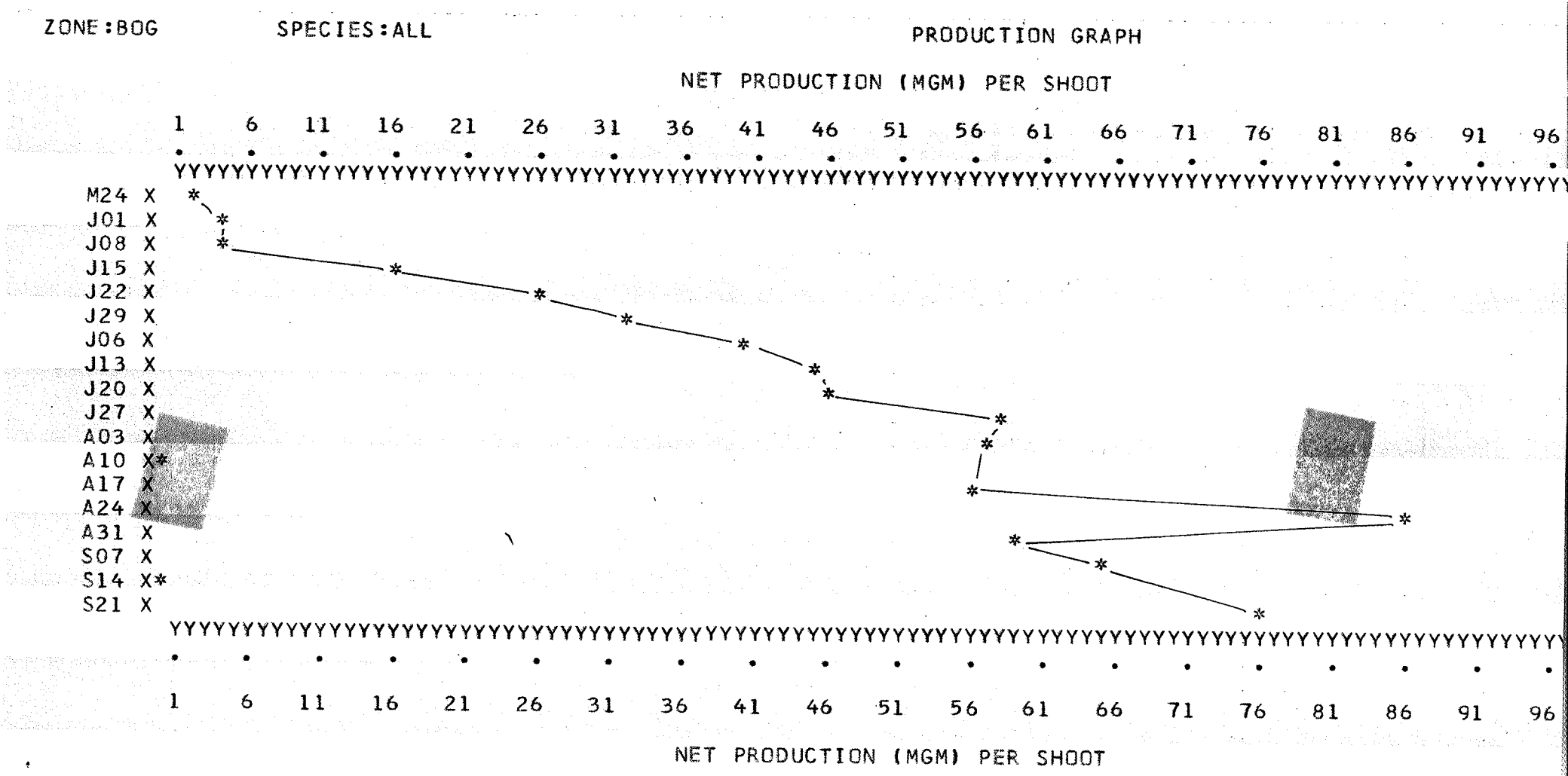

NOTE:PRODUCTION IS 2.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:MUSKEG SPECIES:ALL PRODUCTION GRAPH



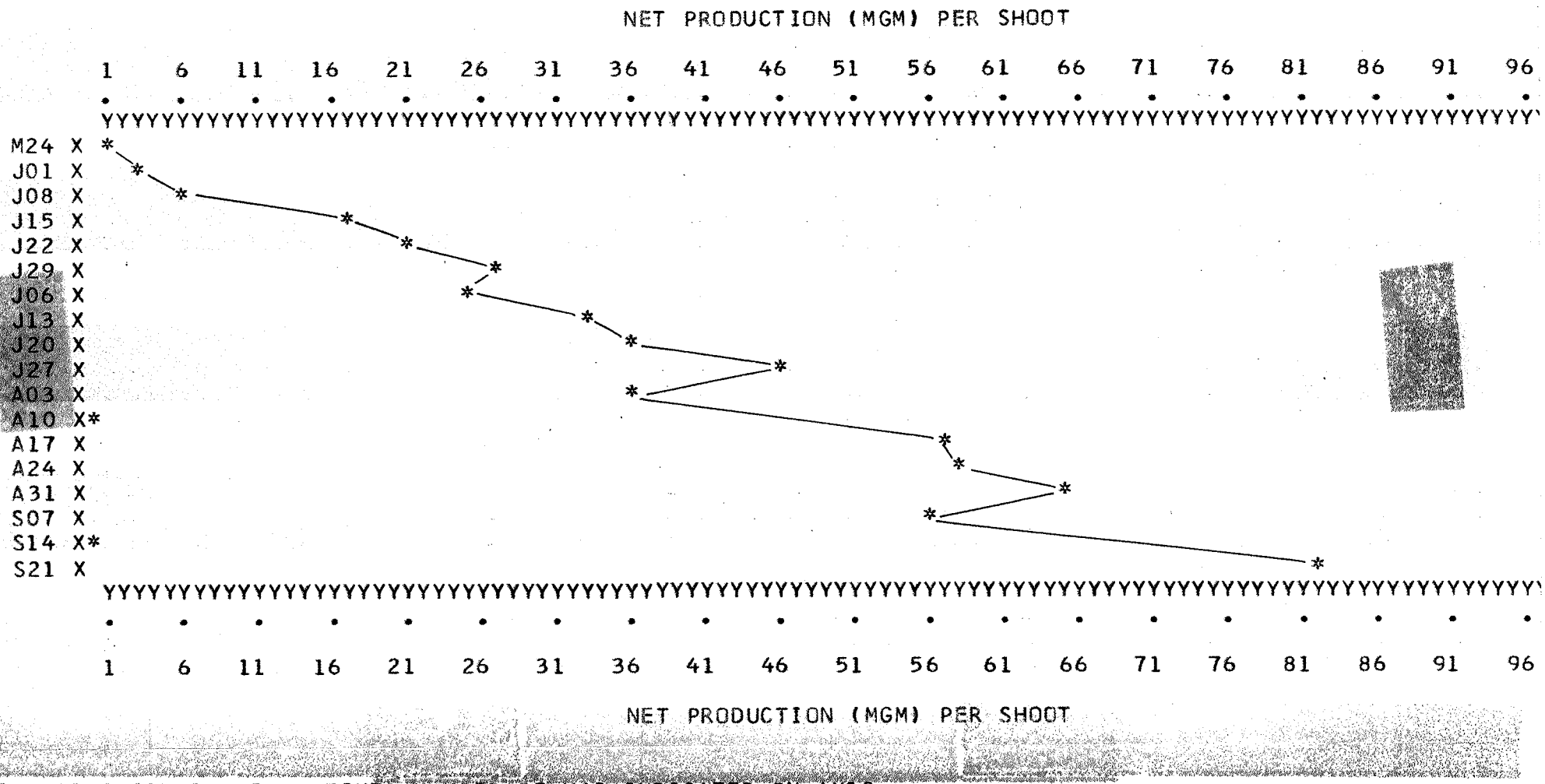

NOTE:PRODUCTION IS 4.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:BOG SPECIES:ALL PRODUCTION GRAPH




NOTE:PRODUCTION IS 3.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

ZONE:LAGG SPECIES:ALL PRODUCTION GRAPH




NOTE:PRODUCTION IS 50.0 TIMES NUMBER OF Y'S INDICATED ON AXIS

TABLE X

MAXIMUM ANNUAL VALUES OF TERMINAL COMPONENT NET PRIMARY PRODUCTION

| Important Species | Bog Forest | | | Muskeg | | | Bog | | | Lagg | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | L | S | FF | L | S | FF | L | S | FF | L | S | FF |
| Group "a" species | | | | | | | | | | | | |
| Ledum groenlandicum | 127.0 | 19.9 | 8.1 | 90.4 | 12.1 | 0.2 | 64.0 | 11.2 | 1.9 | | | |
| Chamaedaphne calyculata | | | | 60.9 | 27.5 | 30.9(*) | 58.5 | 21.4 | 33.6(*) | 76.4 | 30.3 | 28.5(*) |
| Kalmia polifolia | | | | 41.7 | 8.4 | 17.8(*) | 36.6 | 9.1 | 19.6(*) | | | |
| Oxycoccus quadripetalus | | | | | | | 14.2 | 4.6 | 17.2 | | | |
| Vaccinium vitis-idaea var. minus | | | | 43.1 | 14.8 | 16.1 | 32.9 | 10.0 | 16.3 | | | |
| Carex rostrata | | | | | | | | | | 2327.0 | 967.0 | 2.7 |
| Calamagrostis canadensis | | | | | | | | | | 194.0 | 237.0 | 1.3 |
| Group "b" species | | | | | | | | | | | | |
| Picea mariana | 47.6 | 10.9 | - | 68.6 | 18.2 | - | | | | | | |
| Salix bebbiana | | | | | | | | | | 127.0 | 23.3 | 19.7 |
| Salix serissima | | | | | | | | | | 195.0 | 52.3 | 32.5 |

L = maximum leaf weight per individual (mgm.)
S = maximum stem weight per individual (mgm.)
FF = maximum flower-fruit weight per individual (mgm.)
* = value for flower-fruit found on 1969 terminal growth

TABLE XI

DENSITY VALUES FOR IMPORTANT VASCULAR SPECIES FOUND IN THE FOUR VEGETATION ZONES

(A) Group "a" species

| Important Species | Bog Forest $I/m.^2$ | Muskeg $I/m.^2$ | Bog $I/m.^2$ | Lagg $I/m.^2$ |
|---|---|---|---|---|
| Ledum groenlandicum | 192.0 ± 8.5% | 843.2 ± 5.9% | 731.2 ± 5.7% | |
| Chamaedaphne calyculata | | 395.2 ±10.5% | 724.8 ± 6.2% | 920.0 ± 8.8% |
| Kalmia polifolia | | 184.0 ±14.3% | 398.4 ± 6.7% | |
| Vaccinium vitis-idaea var. minus | | 676.8 ± 7.4% | 844.8 ± 7.7% | |
| Oxycoccus quadripetalus | | | 1064.0 ± 9.0% | |
| Carex rostrata | | | | 35.2 ±12.7% |
| Calamagrostis canadensis | | | | 112.0 ±11.5% |

$I/m.^2$ = number of individuals per square meter, ± one standard error expressed as a percent

(B) Group "b" species

| Important Species | Bog Forest (I)x(R) = $I/m.^2$ | | | Muskeg (I)x(R) = $I/m.^2$ | | | Lagg (I)x(R) = $I/m.^2$ | | |
|---|---|---|---|---|---|---|---|---|---|
| Picea mariana | 3182 | 0.782 | 2488.3 | 2585 | 0.197 | 509.2 | | | |
| Salix bebbiana | | | | | | | 189 | 4.90 | 926.1 |
| Salix serissima | | | | | | | 16 | 1.19 | 19.0 |

I = number of individuals per rooted stem
R = number of rooted stems per square meter
$I/m.^2$ = number of individuals per square meter

TABLE XII

VALUES OF MAXIMUM ANNUAL NET PRIMARY PRODUCTION EXPRESSED ON AN AREA BASIS FOR TERMINAL PLANT COMPONENTS

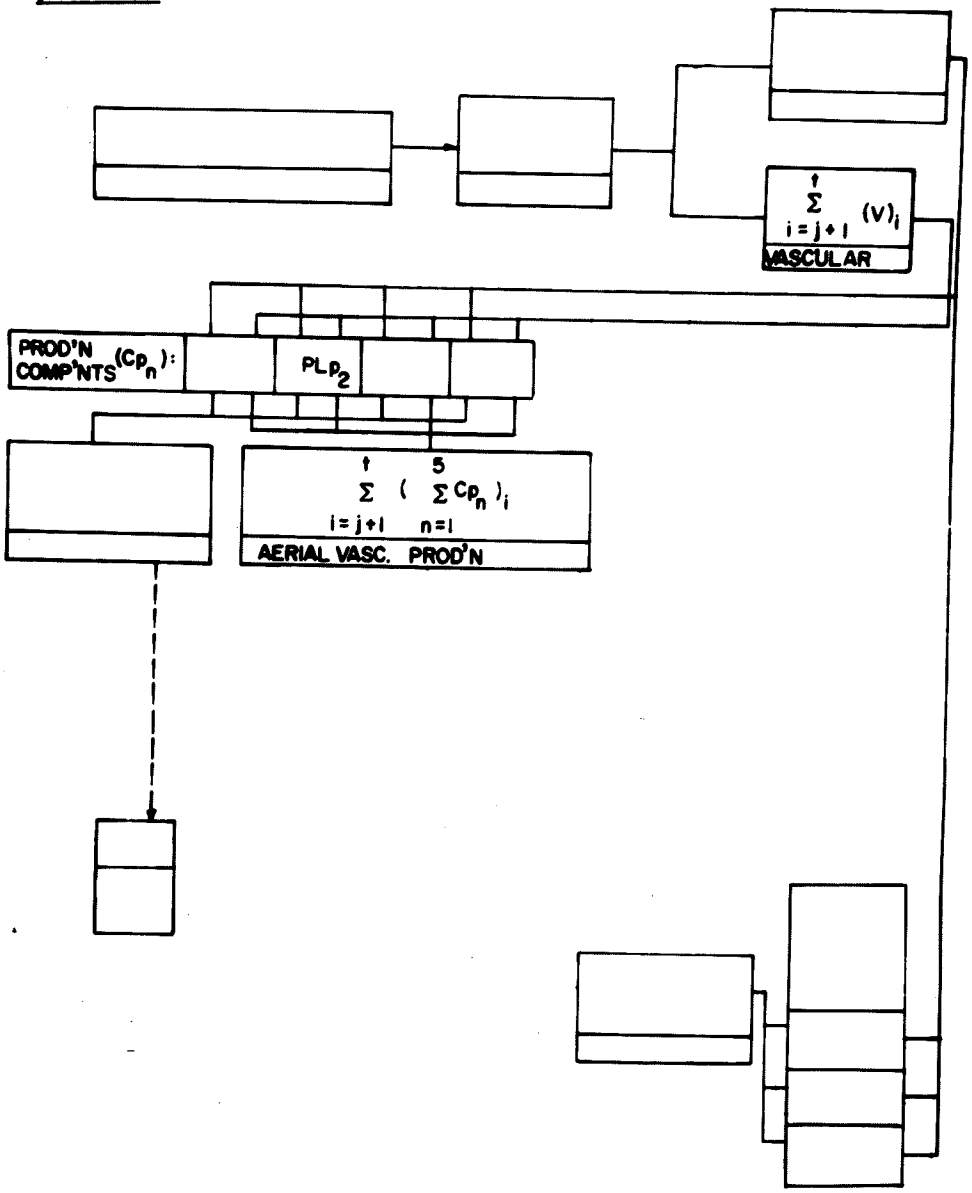
| | Bog Forest | | | Muskeg | | | Bog | | | Lagg | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Important Species | $Lp_1$ | $Sp_4$ | $FFp_3$ | $Lp_1$ | $Sp_4$ | $FFp_3$ | $Lp_1$ | $Sp_4$ | $FFp_3$ | $Lp_1$ | $Sp_4$ | $FFp_3$ |
| Group "a" species | | | | | | | | | | | | |
| Ledum groenlandicum | 24.3 | 3.8 | 1.9 | 76.2 | 10.1 | 0.3 | 46.8 | 8.2 | 1.4 | | | |
| Chamaedaphne calyculata | | | | 24.1 | 10.9 | 12.2 | 42.4 | 15.5 | 24.4 | 70.3 | 27.9 | 26.2 |
| Kalmia polifolia | | | | 7.7 | 1.5 | 3.3 | 14.6 | 3.6 | 7.8 | | | |
| Vaccinium vitis-idaea var. minus | | | | 29.1 | 10.0 | 10.8 | 27.8 | 8.5 | 13.8 | | | |
| Oxycoccus quadripetalus | | | | | | | 15.1 | 4.9 | 18.3 | | | |
| Carex rostrata | | | | | | | | | | 81.9 | 34.0 | 0.1 |
| Calamagrostis canadensis | | | | | | | | | | 21.7 | 26.5 | 0.1 |
| Group "b" species | | | | | | | | | | | | |
| Picea mariana | 118.4 | 27.1 | 0.3 | 34.9 | 9.2 | 0.2 | | | | | | |
| Salix bebbiana | | | | | | | | | | 117.6 | 21.6 | 18.2 |
| Salix serissima | | | | | | | | | | 3.7 | 1.0 | 0.6 |

$Lp_1$ = maximum annual terminal leaf net primary production (gm./m.$^2$)

$Sp_4$ = maximum annual terminal stem net primary production (gm./m.$^2$)

$FFp_3$ = maximum annual terminal flower-fruit net primary production (gm./m.$^2$)

D. 2. The contribution made by leaves produced in previous growing seasons to current net primary production



Species retaining functional leaves for more than one growing season have the opportunity to continue photosynthesizing during winter months, and also in subsequent growing seasons.

Freeland (1944, p. 185) observed photosynthetic activity in Picea mariana during winter months, although only a negligible amount of organic material would be created at this time (Bourdeau, 1959, p. 66). However, during summer months, appreciable increases in the weight of coniferous perennial leaves do take place, as reported by Viro (1955), cited in Bray and Gorham (1964, p. 142).

To determine the dry weight increment in older leaves of P. mariana, for which the life span may be up to twelve years (Fraser and McGuire, 1969, p. 76), samples of two hundred leaves were collected at monthly intervals during the growing season. Trees sampled were those employed in the weekly sampling of terminal components.

Employing the library programme (STATS 25), available at the University of Manitoba Computer Center, all possible mean leaf weights were compared. The t-tests indicated a significant increase in the weight of black spruce leaves produced in previous growing seasons, both in the Bog Forest and Muskeg zones. The average increase for the months of August and September amounted to approximately 24% of the original May

values. Since black spruce was the dominant evergreen species present, then the contribution made to current production by older leaves of group "b" species was assumed to be equal to 24% of their biomass (Table XIII).

In the case of group "a" species, all important ericaceous shrubs involved in this study retained at least some of their leaves for more than one growing season. While Whittaker (1962, p. 361) found that the growth of older leaves in several large ericaceous species in the Great Smoky Mountains was 10% - 16% of the total shoot production, Hadley and Bliss (1964, p. 348), using infra-red gas analysis, observed a negative net photosynthetic rate for perennial leaves of both Ledum groenlandicum and Vaccinium vitis-idaea var. minus.

Samples of two hundred second or third year leaves were collected from the Bog zone at monthly intervals for each of the five important ericoids studied. Comparing all possible mean weights, only September values showed a significant increase. Since the senescent leaves contained in this final sample were collected from the surface of the Bog, a greater percentage of large leaves were present than in previous monthly samples. This sampling problem was responsible for the significant weight increase noted. Therefore, the annual contribution to current net primary production by older leaves of group "a" species was considered to be zero, i.e., $PLp_2 = 0$.

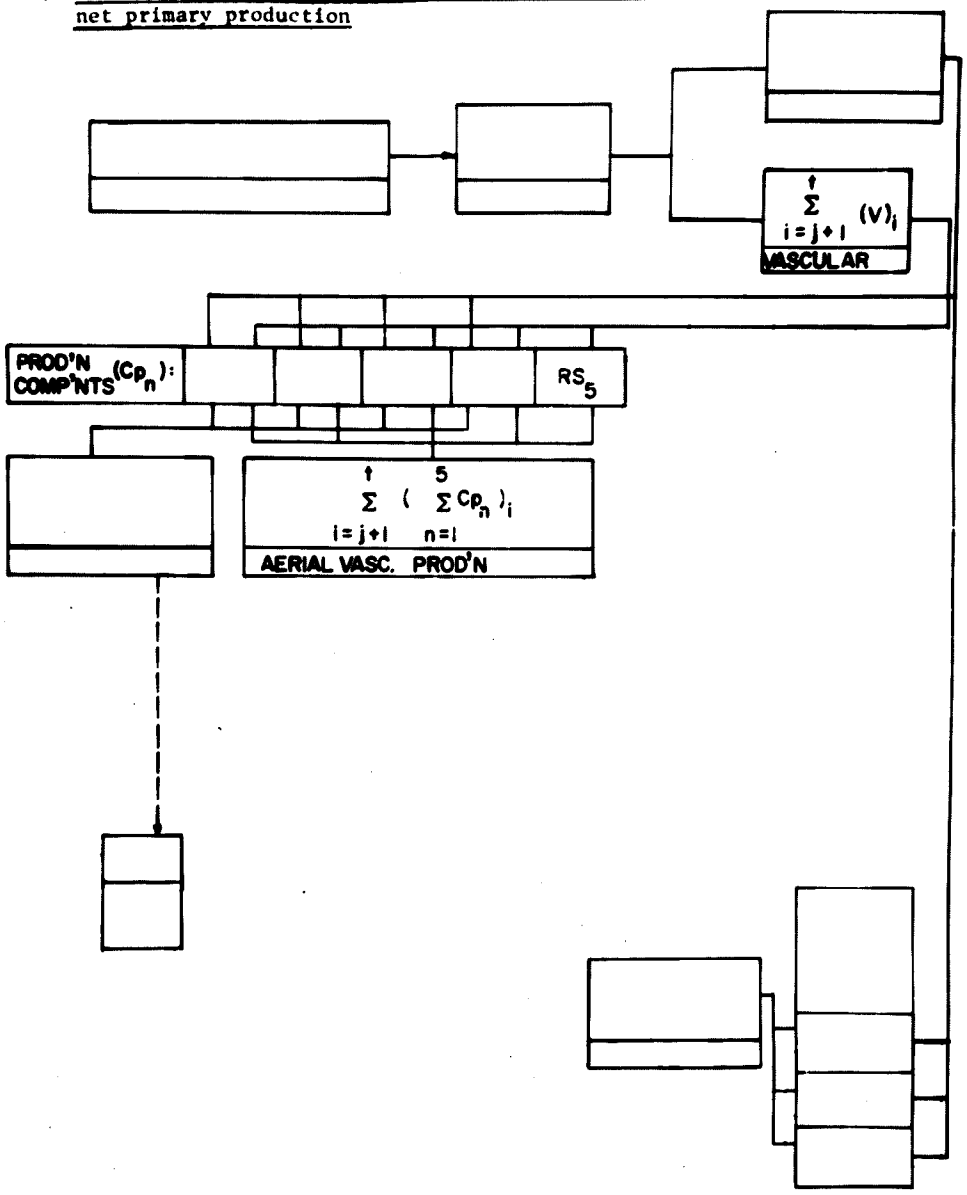
TABLE XIII

CURRENT NET PRIMARY PRODUCTION IN BLACK SPRUCE LEAVES PRODUCED IN PREVIOUS GROWING SEASONS

| Zone | Species | (a) % weight increment by perennial leaves | (b) Weight of perennial leaves per rooted stem gm. | (c) Number of rooted stems per square meter | (a)(b)(c) $PLp_2$ gm./m.$^2$ |
|---|---|---|---|---|---|
| Bog Forest | Picea mariana | 24 | 695.5 | 0.782 | 130.5 |
| Muskeg | Picea mariana | 24 | 327.2 | 0.197 | 15.5 |

$PLp_2$ = maximum annual net primary production by leaves produced in previous growing seasons (gm./m.$^2$)

D. 3. The contribution of secondary growth to aerial net primary production



Woody stems and branches of perennial vascular species increase in weight with each growing season, expanding both in length and in diameter. While the amount of stem elongation can be determined by analyzing terminal new growth, direct calculation of the radial increment in stem and bark is difficult. It may be estimated, however, as the difference between total annual woody increment and the corresponding terminal stem growth.

Total woody increment was calculated by weighing a rooted stem, dividing the observed dry weight by the age[1] of the stem, and multiplying the quotient by the number of rooted stems of this species found in a square meter (Table XIV). In the above calculation, five rooted stems were employed for group "a" species, one stem for each of the group "b" species, all stems harvested at the end of the growing season, i.e., September 28, 1970. The value of terminal stem growth ($Sp_4$) was subtracted from the total woody increment value ($RSp_5 + Sp_4$), to yield an approximate value for radial stem and bark growth (Table XV). The presence of two negative $RSp_5$ values in Table XV indicated that this procedure was not entirely satisfactory. Therefore, $RSp_5$ values should be considered as estimates only.

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[1] age = maximum number of annual increments on a stem (group "a" species) or the number of annual rings (group "b" species)

TABLE XIV

TOTAL ANNUAL WOODY INCREMENT IN THE IMPORTANT VASCULAR SPECIES STUDIES

| Important Species | Bog Forest (W) | x (#) | = ∑ | Muskeg (W) | x (#) | = ∑ | Bog (W) | x (#) | = ∑ | Lagg (W) | x (#) | = ∑ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Group "a" species | | | | | | | | | | | | |
| Ledum groenlandicum | 426.0 | 62.5 | 26.6 | 174.0 | 267.2 | 46.5 | 68.4 | 291.2 | 19.9 | | | |
| Chamaedaphne calyculata | | | | 111.0 | 190.4 | 21.1 | 121.0 | 324.8 | 39.3 | 514.0 | 254.4 | 130.8 |
| Kalmia polifolia | | | | 46.1 | 52.8 | 2.4 | 54.3 | 157.3 | 8.5 | | | |
| Vaccinium vitis-idaea var. minus | | | | 15.6 | 481.6 | 7.5 | 15.0 | 739.2 | 11.1 | | | |
| Oxycoccus quadripetalus | | | | | | | 19.7 | 862.4 | 17.0 | | | |
| Group "b" species | | | | | | | | | | | | |
| Picea mariana | 68200.0 | 0.782 | 53.3 | 39400.0 | 0.197 | 7.8 | | | | | | |
| Salix bebbiana | | | | | | | | | | 17000.0 | 4.90 | 83.3 |
| Salix serissima | | | | | | | | | | 5200.0 | 1.16 | 6.0 |

W = average annual total woody increment (mgm./rooted stem)
# = number of rooted stems per square meter
∑ = total annual woody increment (gm./m.$^2$) = $\sum_{n=4}^{5} {}^{C}p_n$

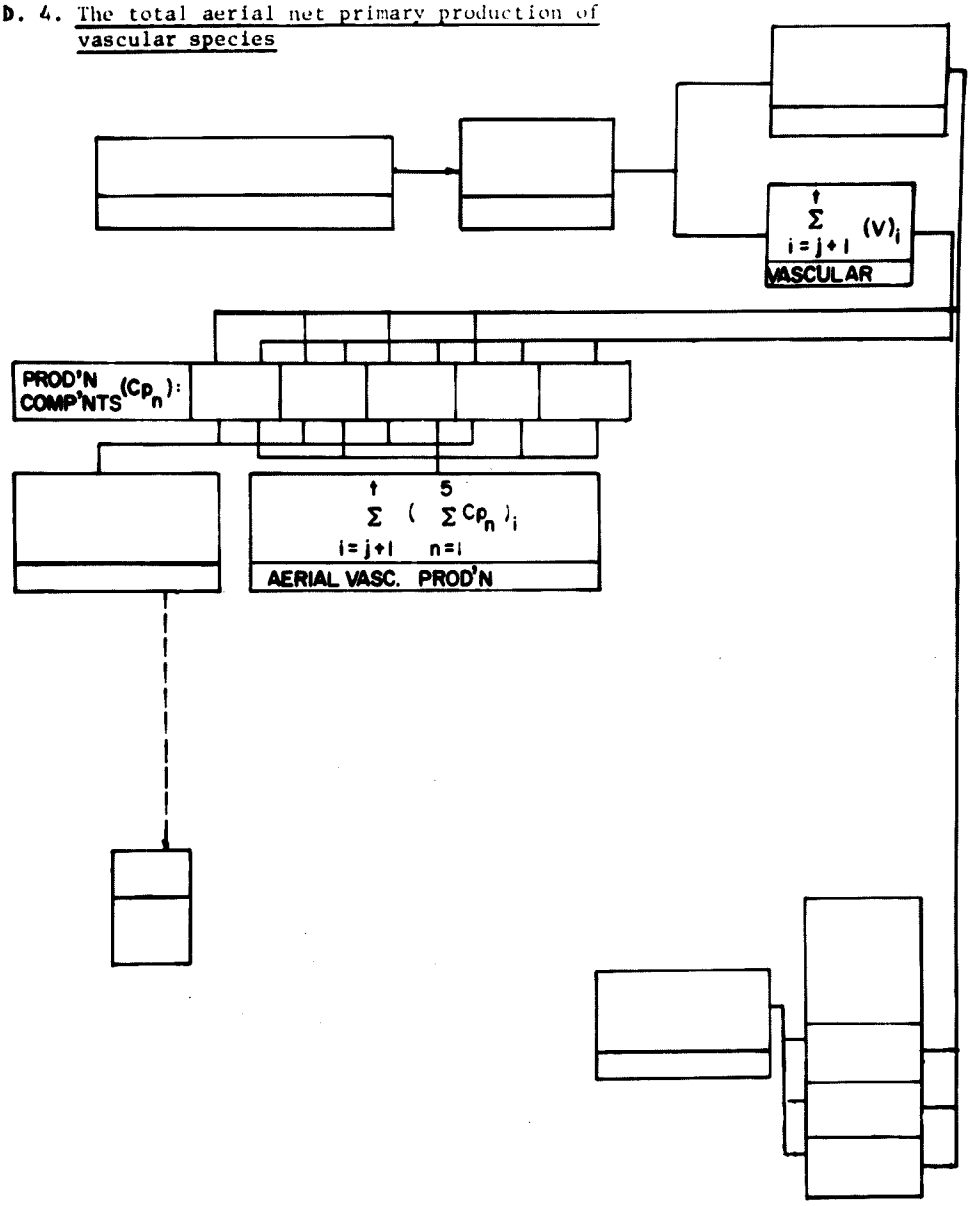
TABLE XV

THE ANNUAL RADIAL INCREMENT IN IMPORTANT VASCULAR SPECIES HAVING WOODY STEMS

| Important Species | Bog Forest | | Muskeg | | Bog | | Lagg | |
|---|---|---|---|---|---|---|---|---|
| | $RSp_5+Sp_4$ | $RSp_5$ | $RSp_5+Sp_4$ | $RSp_5$ | $RSp_5+Sp_4$ | $RSp_5$ | $RSp_5+Sp_4$ | $RSp_5$ |
| Group "a" species | | | | | | | | |
| Ledum groenlandicum | 26.6 | 22.8 | 46.5 | 36.4 | 19.9 | 11.7 | | |
| Chamaedaphne calyculata | | | 21.1 | 10.2 | 39.3 | 23.8 | 130.8 | 102.9 |
| Kalmia polifolia | | | 2.4 | 0.9 | 8.5 | 4.9 | | |
| Vaccinium vitis-idaea var. minus | | | 7.5 | - 2.5 | 11.1 | 2.6 | | |
| Oxycoccus quadripetalus | | | | | 17.0 | 12.1 | | |
| Group "b" species | | | | | | | | |
| Picea mariana | 53.3 | 26.2 | 7.8 | - 1.4 | | | | |
| Salix bebbiana | | | | | | | 83.3 | 61.7 |
| Salix serissima | | | | | | | 6.0 | 5.0 |

$Sp_4$ = maximum annual net primary production of terminal new stems and bark ($gm./m.^2$)
$RSp_5$ = maximum annual net primary production in stems and bark produced in previous years ($gm./m.^2$)

D. 4. The total aerial net primary production of vascular species



At this point values have been derived for each of the aerial components contributing to the production of dry matter. The data is summarized in Table XVI. Comparing the relative contributions of aerial components to total production, the only consistency found in all species was that current leaves were most important. The relative importance of the other components varied from species to species.

It would be of benefit to compare the production values observed in the current study with those recorded in other situations. Unfortunately, there is very little data with which these production values can be compared. The fact that production values depend both on the weight of an individual and on the number of such individuals found per unit area, also makes it difficult to compare production values given only in terms of weight per unit area. For example, Traczyk (1967, p. 845) reported that the net production of Vaccinium vitis-idaea L. in two Pinus associations ranged from 0.15 to 0.83 gm./m.$^2$, considerably lower than the 47.4 to 52.7 gm./m.$^2$ range indicated for aerial component production by Vaccinium vitis-idaea var. minus in the Muskeg and Bog zones. Yet, production by a single plant in Traczyk's study was found to range from 0.067 to 0.083 gm., with the corresponding range at Elma 0.071 - 0.098 gm. Thus, it is necessary to have both individual production values

TABLE XVI

SUMMARY OF AERIAL COMPONENT NET PRIMARY PRODUCTION IN EACH OF THE IMPORTANT SPECIES STUDIED

| | $Lp_1$ | $PLp_2$ | $FFp_3$ | $Sp_4$ | $RSp_5$ | $\sum_{n=1}^{5} Cp_n$ | Rank |
|---|---|---|---|---|---|---|---|
| | gm./m.$^2$ | gm./m.$^2$ | gm./m.$^2$ | gm./m.$^2$ | gm./m.$^2$ | gm./m.$^2$ | |
| (A) Zone: Bog Forest | | | | | | | |
| Group "a" species | | | | | | | |
| Ledum groenlandicum | 24.3 (46%)* | 0.0 (0%) | 1.9 (4%) | 3.8 (7%) | 22.8 (43%) | 52.8 | 2 |
| Group "b" species | | | | | | | |
| Picea mariana | 118.4 (39%) | 130.5 (43%) | 0.3 (0%) | 27.1 (9%) | 26.2 (9%) | 302.5 | 1 |
| (B) Zone: Muskeg | | | | | | | |
| Group "a" species | | | | | | | |
| Ledum groenlandicum | 76.2 (62%) | 0.0 (0%) | 0.3 (1%) | 10.1 (8%) | 36.4 (29%) | 123.0 | 1 |
| Chamaedaphne calyculata | 24.1 (42%) | 0.0 (0%) | 12.2 (21%) | 10.9 (19%) | 10.2 (18%) | 57.4 | 3 |
| Vaccinium vitis-idaea var. minus | 29.1 (62%) | 0.0 (0%) | 10.8 (22%) | 10.0 (21%) | -2.5 (-5%) | 47.4 | 4 |
| Kalmia polifolia | 7.7 (57%) | 0.0 (0%) | 3.3 (25%) | 1.5 (11%) | 0.9 (7%) | 13.4 | 5 |
| Group "b" species | | | | | | | |
| Picea mariana | 34.9 (60%) | 15.5 (26%) | 0.2 (0%) | 9.2 (16%) | -1.4 (-2%) | 58.4 | 2 |

*Figures in parenthesis indicate the percentage of total aerial net primary production

$Lp_1$ = new leaves; $PLp_2$ = perennial leaves; $FFp_3$ = flower-fruits; $Sp_4$ = new stems; $RSp_5$ = radial stem increment

TABLE XVI (continued)

| | $Lp_1$ | $PLp_2$ | $FFp_3$ | $Sp_4$ | $RSp_5$ | $\sum_{n=1}^{5} Cp_n$ | Rank |
|---|---|---|---|---|---|---|---|
| | gm./m.$^2$ | gm./m.$^2$ | gm./m.$^2$ | gm./m.$^2$ | gm./m.$^2$ | gm./m.$^2$ | |
| (C) Zone: Bog | | | | | | | |
| Group "a" species | | | | | | | |
| Chamaedaphne calyculata | 42.4 (39%)* | 0.0 (0%) | 24.4 (24%) | 15.5 (15%) | 23.8 (22%) | 106.1 | 1 |
| Ledum groenlandicum | 46.8 (69%) | 0.0 (0%) | 1.4 (2%) | 8.2 (12%) | 11.7 (17%) | 68.1 | 2 |
| Vaccinium vitis-idaea var. minus | 27.8 (53%) | 0.0 (0%) | 13.8 (26%) | 8.5 (16%) | 2.6 (5%) | 52.7 | 3 |
| Oxycoccus quadripetalus | 15.1 (30%) | 0.0 (0%) | 18.3 (36%) | 4.9 (10%) | 12.1 (24%) | 50.4 | 4 |
| Kalmia polifolia | 14.6 (47%) | 0.0 (0%) | 7.8 (25%) | 3.6 (12%) | 4.9 (16%) | 30.9 | 5 |
| (D) Zone: Lagg | | | | | | | |
| Group "a" species | | | | | | | |
| Chamaedaphne calyculata | 70.3 (31%) | 0.0 (0%) | 26.2 (12%) | 27.9 (12%) | 102.9 (45%) | 227.3 | 1 |
| Carex rostrata | 81.9 (71%) | 0.0 (0%) | 0.1 (0%) | 34.0 (29%) | 0.0 (0%) | 116.0 | 3 |
| Calamagrostis canadensis | 21.7 (45%) | 0.0 (0%) | 0.1 (0%) | 26.5 (55%) | 0.0 (0%) | 48.3 | 4 |
| Group "b" species | | | | | | | |
| Salix bebbiana | 117.6 (54%) | 0.0 (0%) | 18.2 (8%) | 21.6 (10%) | 61.7 (28%) | 219.1 | 2 |
| Salix serissima | 3.7 (33%) | 0.0 (0%) | 0.6 (5%) | 6.0 (53%) | 1.0 (9%) | 11.3 | 5 |

*Figures in parenthesis indicate the percentage of total aerial net primary production
$Lp_1$ = new leaves; $PLp_2$ = perennial leaves; $FFp_3$ = flower-fruits; $Sp_4$ = new stems; $RSp_5$ = radial stem increment

and density values to correctly assess production potential for a species when it is found either in diverse geographic locations, or in different ecosystem types.

An additional column in Table XVI indicates the relative importance of a species to zonal production. This importance ranking closely parallels the ranking produced earlier, based on relative frequency values (Table III). This agreement verifies the assumption that a species' relative productivity is proportional to its frequency of occurrence.

Total aerial production for important vascular species is found in the first column of Table XVII. Not all species were represented in these production figures, since only species having a relative frequency value greater than 5% were studied on an individual basis.

To obtain an estimate of the production contributed by other group "a" species, their terminal new growth was harvested at each sampling date, and the weight expressed as a percentage of that of important species encountered in the same quadrats. At the end of the growing season an average percentage value was determined and the calculated aerial production sum increased by this percentage (Table XVII).

For group "b" species, it was assumed that the productivity per rooted stem of all broad-leaved species approached

TABLE XVII

TOTAL AERIAL NET PRIMARY PRODUCTION FOR ALL VASCULAR SPECIES OCCURRING IN THE FOUR VEGETATION ZONES

(A) Group "a" species

| Zone | (a) $\sum_{n=1}^{5} Cp_n$ Important Species gm./m.$^2$ | (b) Contribution by Other Species % ± One Standard Error | (a)+(a)(b) $\sum_{n=1}^{5} Cp_n$ All Species gm./m.$^2$ |
|---|---|---|---|
| Bog Forest | 52.8 | 21.3 ± 6.9 | 64.0 |
| Muskeg | 241.2 | 5.3 ± 1.0 | 253.9 |
| Bog | 308.2 | 2.7 ± 0.6 | 316.4 |
| Lagg | 391.6 | 15.6 ± 3.9 | 452.7 |

(B) Group "b" species

| Zone | (a) $\sum_{n=1}^{5} Cp_n$ Important Species gm./m.$^2$ | (b) $\frac{\text{\# of rooted stems/m.}^2 \text{ for all species}}{\text{\# of rooted stems/m.}^2 \text{ for important species}}$ | (a)(b) $\sum_{n=1}^{5} Cp_n$ All Species gm./m.$^2$ |
|---|---|---|---|
| Bog Forest | 302.5 | 0.782/0.782 | 302.5 |
| Muskeg | 58.4 | 0.244/0.197 | 71.8 |
| Bog | - | - | - |
| Lagg | 230.4 | 13.09/6.06 | 497.7 |

the mean value calculated for Salix bebbiana and S. serissima, and similarly that the production figure of needle-leaved species approached that of Picea mariana. A total production value for group "b" species was arrived at by multiplying the calculated production figure per rooted stem by the total number of rooted stems of all species found in a square meter (Table XVII).

Zonal aerial production totals for group "a" species showed a trend consistent with the spatial distribution of the four zones, i.e., Lagg > Bog > Muskeg > Bog Forest. Group "b" species production was also greatest in the Lagg zone, with a trend in direct opposition to group "a" species production values evident in the remaining three zones, i.e., Bog < Muskeg < Bog Forest. As a result, total aerial production values in the Bog, Muskeg and Bog Forest zones were all quite similar (Table XVIII). Production in the Lagg zone, 950 gm./m.$^2$, was almost three times as great.

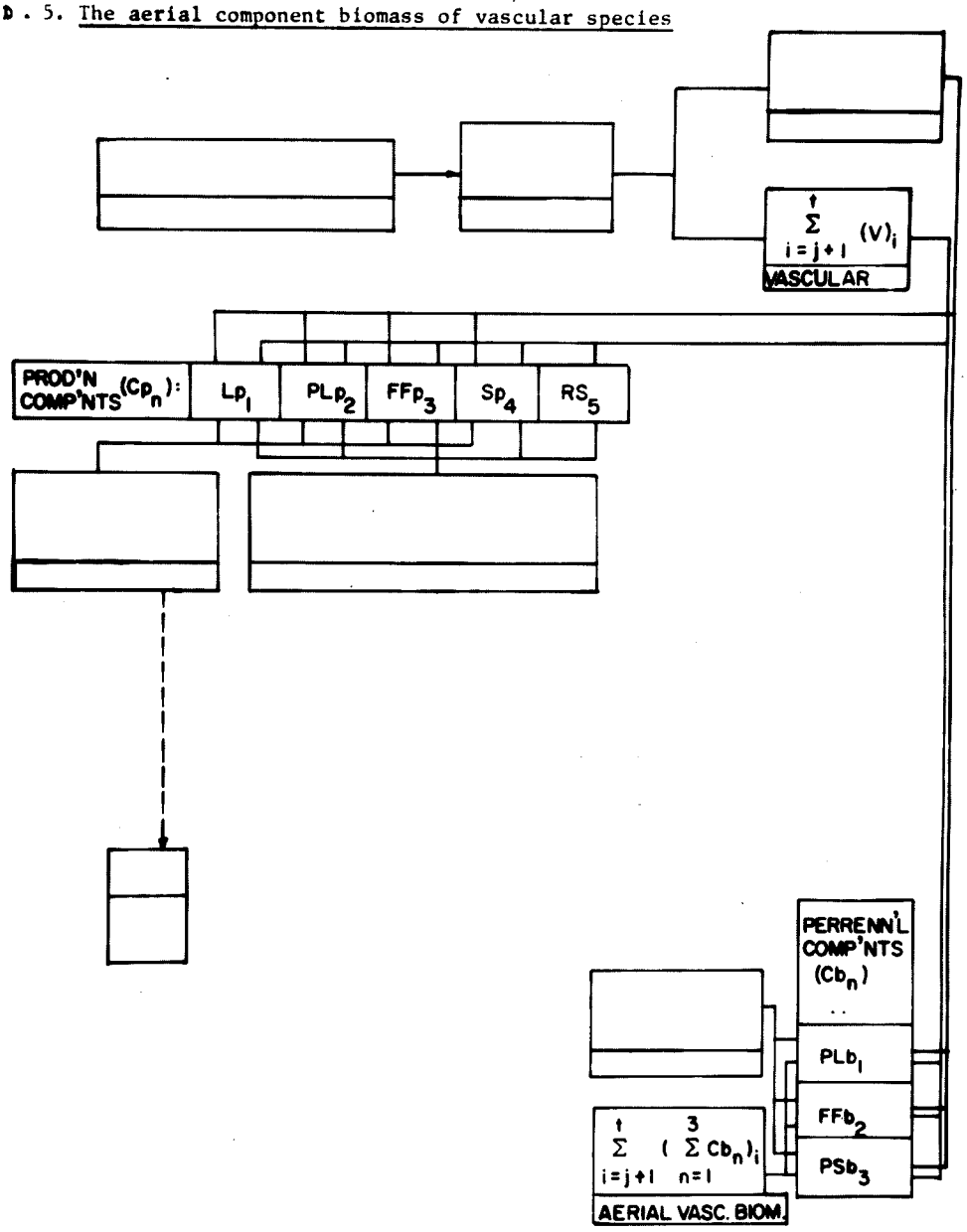
TABLE XVIII

TOTAL AERIAL VASCULAR PRODUCTION

| Zone | (a) $\sum_{n=1}^{5} Cp_n$ Group "a" Species gm./m.$^2$ | (b) $\sum_{n=1}^{5} Cp_n$ Group "b" Species gm./m.$^2$ | (a)+(b) AERIAL VASC. PROD'N gm./m.$^2$ |
|---|---|---|---|
| Bog Forest | 64.0 | 302.5 | 366.5 |
| Muskeg | 253.9 | 71.8 | 325.7 |
| Bog | 316.4 | - | 316.4 |
| Lagg | 452.7 | 497.7 | 950.4 |

$$\text{AERIAL VASC. PROD'N} = \sum_{i=j+1}^{t} \left( \sum_{n=1}^{5} Cp_n \right)_i$$

D . 5. The aerial component biomass of vascular species



Biomass values of aerial plant components produced in previous years were obtained from clippings made at each weekly sampling date. By combining these values with the weight of current terminal production, a weekly value for the total biomass (TB) of a single plant was derived for each species:

$$TB = \frac{\sum_{n=1}^{5} Cp_n + \sum_{n=1}^{3} Cb_n}{\text{number of rooted stems in the weekly sample}}$$

Due to differences in the amount of woody biomass contained in the weekly samples values of TB varied considerably over the growing season. Therefore, in calculating total biomass for plants of each species on an area basis the average of weekly TB values was multiplied by the mean number of rooted stems found in one square meter (Table XIX).

A biomass value for aerial components of all vascular species (Table XX) was determined with the following equation:

$$\frac{\text{aerial biomass of all vascular species}}{\text{aerial biomass of important vascular species}} = \frac{\text{total aerial production of all vascular species}}{\text{total aerial production of important vascular species}}$$

TABLE XIX

AERIAL BIOMASS VALUES OF IMPORTANT VASCULAR SPECIES FOUND IN EACH OF THE VEGETATION ZONES STUDIED

| | Bog Forest | | | Muskeg | | | Bog | | | Lagg | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $(\overline{X})$ | x (#) | = $\sum$ | $(\overline{X})$ | x (#) | = $\sum$ | $(\overline{X})$ | x (#) | = $\sum$ | $(\overline{X})$ | x (#) | = $\sum$ |
| Group "a" species | | | | | | | | | | | | |
| Ledum groenlandicum | 2.15 ±16.0% | 62.5 ±8.3% | 134.5 | 0.887 ±5.3% | 267.2 ±7.9% | 237.0 | 0.441 ±12.2% | 291.2 ±6.5% | 128.4 | | | |
| Chamaedaphne calyculata | | | | 0.738 ±7.9% | 190.4 ±10.7% | 140.5 | 0.445 ±8.2% | 324.8 ±6.2% | 151.0 | 1.77 ±10.1% | 254.4 ±7.9% | 452.1 |
| Kalmia polifolia | | | | 0.523 ±13.8% | 52.8 ±14.9% | 27.6 | 0.282 ±13.1% | 157.3 ±8.5% | 44.0 | | | |
| Vaccinium vitis-idaea var. minus | | | | 0.117 ±5.1% | 481.6 ±6.6% | 56.3 | 0.072 ±4.9% | 739.2 ±7.0% | 53.4 | | | |
| Oxycoccus quadripetalus | | | | | | | 0.041 ±7.1% | 862.4 ±11.7% | 35.5 | | | |
| Carex rostrata | | | | | | | | | | 1.24 ±18.4% | 35.2 ±12.7% | 43.5 |
| Calamangrostis canadensis | | | | | | | | | | 0.207 ±17.0% | 112.0 ±11.5% | 23.2 |

$\overline{X}$ = mean aerial biomass per rooted stem (gm. ± one standard error expressed as a percent)
\# = number of rooted stems found in a square meter ± one standard error expressed as a percent
$\sum = \sum_{n=1}^{5} Cp_n + \sum_{n=1}^{3} Cb_n$ , total aerial biomass in $gm.m.^2$

TABLE XIX (continued)

| | Bog Forest | | | Muskeg | | | Bog | | | Lagg | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $(\overline{X})$ | x (#) | $= \sum$ | $(\overline{X})$ | x (#) | $= \sum$ | $(\overline{X})$ | x (#) | $= \sum$ | $(\overline{X})$ | x (#) | $= \sum$ |
| Group "b" species | | | | | | | | | | | | |
| Picea mariana | 5353.0 | 0.782 | 4186.0 | 1867.0 | 0.197 | 367.8 | | | | | | |
| Salix serissima | | | | | | | | | | 57.7 | 1.16 | 66.9 |
| Salix bebbiana | | | | | | | | | | 203.7 | 4.90 | 998.2 |

$\overline{X}$ = mean aerial biomass per rooted stem (gm. ± one standard error expressed as a percent)
\# = number of rooted stems found in a square meter ± one standard error expressed as a percent
$\sum = \sum_{n=1}^{5} Cp_n + \sum_{n=1}^{3} Cb_n$ , total aerial biomass in gm./m.$^2$

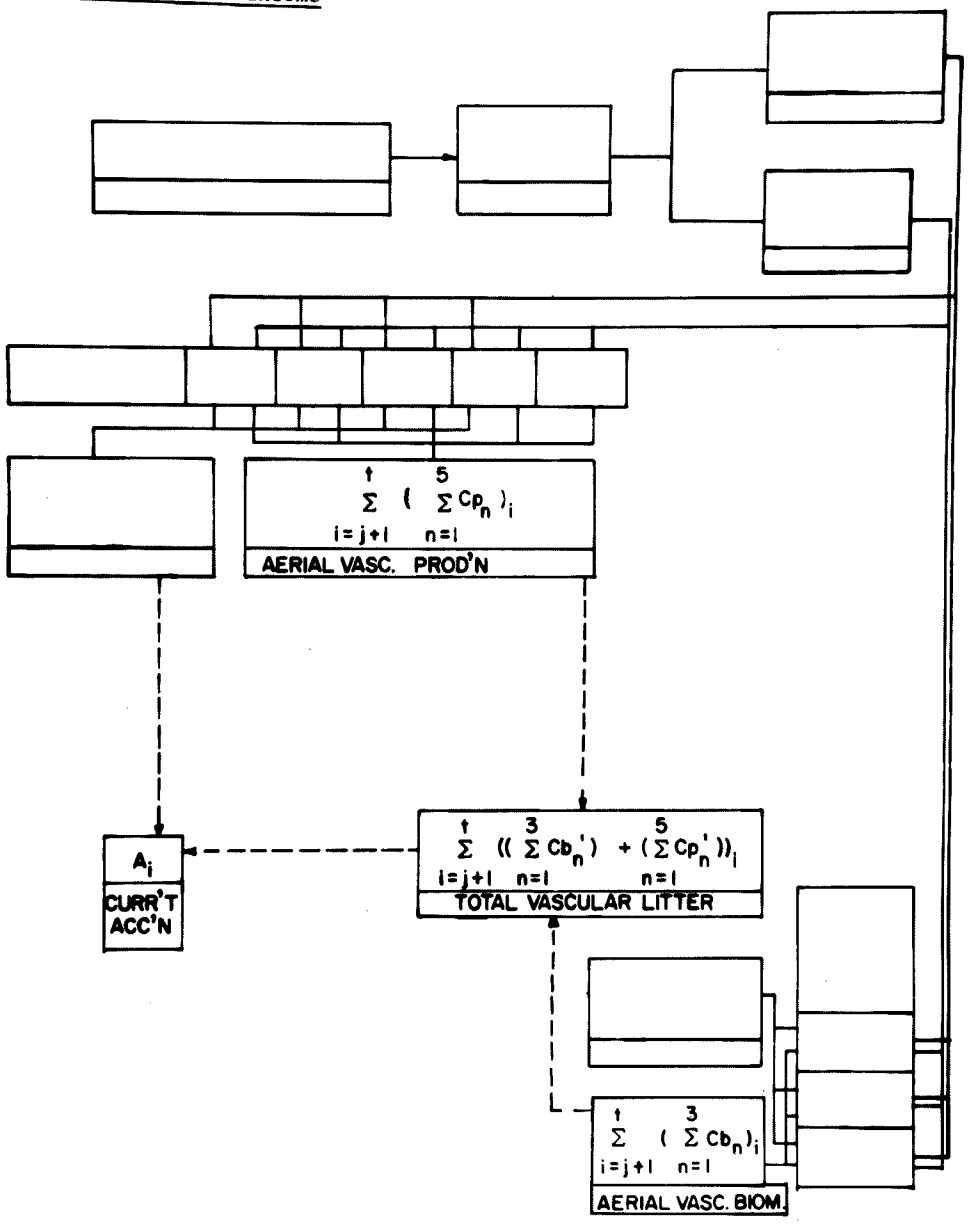
TABLE XX

TOTAL AERIAL BIOMASS OF VASCULAR SPECIES

| Zone | (a) $(\sum_{n=1}^{5} Cp_n)+(\sum_{n=1}^{3} Cb_n)$ For Important Species gm./m.$^2$ | (b) $\frac{\text{aerial production by all vascular species}}{\text{aerial production by important vascular species}}$ | (a)(b) $\sum$ gm./m.$^2$ |
|---|---|---|---|
| Bog Forest | 4320.5 | 1.031 | 4454.5 |
| Muskeg | 829.2 | 1.087 | 901.3 |
| Bog | 412.6 | 1.026 | 423.3 |
| Lagg | 1583.9 | 1.527 | 2418.8 |

$$\sum = \sum_{i=j+1}^{t} [(\sum_{n=1}^{5} Cp_n) + (\sum_{n=1}^{3} Cb_n)]_i \text{ , aerial biomass total}$$

D. 6. The contribution of aerial vascular components to accumulation income



Of the aerial plant components contributing to the production of dry matter, it can be expected that leaves, reproductive structures, and some branch wood and bark will be lost each year through death. In the case of deciduous species it is the leaf material produced in the current growing season that is lost, while in semi-deciduous and perennial species leaves formed in previous growing seasons are lost. It was assumed that the number of leaves falling from perennial portions was equal to the number of newly produced leaves. Since leaf material was lost from either current or perennial portions but not both, then the annual amount of leaf litter was determined from the production values calculated for the new leaf component ($Lp_1$). However, translocation of material in senescing leaves must also be considered, since it reduces the amount contributable by new leaves. The amount of weight lost from leaves during senescence was calculated for each species studied on an individual basis. At three sampling dates in 1970 (July 20, August 24, September 21), two hundred new leaves of each of the important vascular species were collected, their dry weight determined, and the largest of the three weights used to calculate the maximum single leaf weight in each of these species. Senescing leaves of the same species were also collected on August 24th, when the leaves were still attached to living stems, and on September 28th

when the leaves had fallen. Unfortunately, ericoid leaf samples collected from the bog's surface contained a greater percentage of large leaves than did previous samples, since after falling small leaves were difficult to collect. This resulted in September leaf values being equal to, or significantly greater than, the maximum new leaf weights. Therefore, August values of perennial leaf weight were used to determine the senescence weight loss. Since Oland (1963, p. 686) found the dry weight loss from leaves to take place during a period three to four weeks prior to abscission, then it was considered valid to employ these August values to represent minimum leaf weights.

Using an unpaired t-test the maximum and minimum leaf weights were compared. These values are listed in Table XXI. If a significant decrease was indicated, then the percentage lost during senescence was calculated for the species as follows:

$$\frac{\text{maximum observed leaf weight} - \text{minimum observed leaf weight}}{\text{maximum observed leaf weight}} \times 100\%$$

Comparing the observed senescence losses with existing literature values, the 17% loss reported by Mutoh et al (1968, p. 72) for the grass Miscanthus sp., was much less than 43.5% lost by Calamagrostis canadensis. Bray and Gorham (1964, p. 142) cite a study by Viro (1955) in which 19 - 23% of dry weight in deciduous angiosperm leaves was lost on senescence,

TABLE XXI

SENESCENCE WEIGHT LOSS IN LEAVES OF IMPORTANT VASCULAR SPECIES

| Important Species | Zone Sampled | M | S | D | % Weight Loss On Senescence |
|---|---|---|---|---|---|
| Group "a" species | | | | | |
| *Ledum groenlandicum* | Bog | 9.53 | 8.15 | - | 14.4 |
| *Chamaedaphne calyculata* | Bog | 7.04 | 4.98 | - | 43.4 |
| *Kalmia polifolia* | Bog | 5.16 | 3.74 | - | 27.5 |
| *Vaccinium vitis-idaea* var. *minus* | Bog | 3.92 | 4.33 | 0 | 0 |
| *Oxycoccus quadripetalus* | Bog | 1.69 | 1.65 | 0 | 0 |
| *Calamagrostis canadensis* | Lagg | 38.4 | 21.8* | - | 43.5 |
| *Carex rostrata* | Lagg | 258.0 | 216.0* | - | 16.3 |
| Group "b" species | | | | | |
| *Picea mariana* | Muskeg | 1.82 | 1.76 | 0 | 0 |
| *Picea mariana* | Bog Forest | 1.05 | 1.04 | 0 | 0 |
| *Salix bebbiana* | Lagg | 24.0 | 17.2* | - | 28.3 |
| *Salix serissima* | Lagg | 31.8 | 45.7* | + | -- |

M = maximum leaf dry weight (mgm.) observed during the growing season
* = senescent leaf dry weights (mgm.) recorded on September 28, 1970
S = senescent leaf dry weight (mgm.) recorded on August 24, 1970
D = difference between "M" and "S" leaf weights indicated by an unpaired t-test (P=0.05), where 0 = no difference; - = significant decrease; + = significant increase

slightly less than the 28% loss determined for Salix bebbiana. The fact that perennial leaves of Picea mariana continue to gain weight in subsequent growing seasons accounts for the fact that senescent perennial leaves showed no appreciable difference in weight from the maximum weight of current leaves.

Although senescence values were calculated from changes in leaf weight only, reproductive structures also lose weight when senescing. Therefore, the senescence correction was applied to both leaf ($Lp_1$) and flower-fruit ($FFp_3$) weights (Table XXII). Summing the resulting values for important species and correcting the total for the contribution by "other" species provided an estimate of total leaf and flower-fruit material added annually to peat.

Bray & Gorham (1964, p. 119) estimated that in both angiosperm and gymnosperm forests leaf litter represented an average of 70% of the total annual litter increment. Therefore, based on the relative values of leaf and flower-fruit production, it was estimated that reproductive structures contributed 11% to this total, while the remainder of 19% was contributed by woody tissues. To calculate the total annual litter increment, the weight of leaf and flower-fruit litter was multiplied by the value fraction 100/81 (Table XXIII).

Corrected values indicated that the greatest amount of

TABLE XXII

POST-SENESCENCE DRY WEIGHT OF LEAF AND FLOWER-FRUIT COMPONENTS ADDED ANNUALLY TO THE PEATLAND'S SURFACE

| | (a) $Lp_1+FFp_3$ gm./m.$^2$ | (b) % Lost on Senescence | (a) $-$ (a)(b) $Lp_1'+FFp_3'$ gm./m.$^2$ | (c) | $[\sum(a - ab)](c) = (d)$ gm./m.$^2$ |
|---|---|---|---|---|---|
| (A) Zone : Bog Forest | | | | 1.031 | 145.5 |
| Group "a" species | | | | | |
| Ledum groenlandicum | 26.2 | 14.4 | 22.4 | | |
| Group "b" species | | | | | |
| Picea mariana | 118.7 | 0 | 118.7 | | |
| (B) Zone : Muskeg | | | | 1.087 | 183.8 |
| Group "a" species | | | | | |
| Ledum groenlandicum | 76.5 | 14.4 | 65.5 | | |
| Chamaedaphne calyculata | 36.3 | 43.4 | 20.5 | | |
| Kalmia polifolia | 11.0 | 27.5 | 8.0 | | |
| Vaccinium vitis-idaea var. minus | 39.9 | 0 | 39.9 | | |
| Group "b" species | | | | | |
| Picea mariana | 35.1 | 0 | 35.1 | | |

(c) = correction factor for "other" species, i.e., $\frac{\text{aerial prod'n by all vasc. species}}{\text{aerial prod'n by important vasc. species}}$

(d) = $\sum_{i=j+1}^{t} (Lp_1' + FFp_3')_i$ , total leaf and flower-fruit litter weight in important species

' = at death

TABLE XXII (continued)

| | (a) $Lp_1+FFp_3$ gm./m.$^2$ | (b) % Lost on Senescence | (a) - (a)(b) $Lp_1+FFp_3$ gm./m.$^2$ | (c) | $[\sum(a - ab)]$ (c) = (d) gm./m.$^2$ |
|---|---|---|---|---|---|
| (C) Zone : Bog | | | | 1,026 | 174.8 |
| Group "a" species | | | | | |
| Ledum groenlandicum | 48.2 | 14.4 | 41.3 | | |
| Chamaedaphne calyculata | 66.8 | 43.4 | 37.8 | | |
| Kalmia polifolia | 22.4 | 27.5 | 16.3 | | |
| Vaccinium vitis-idaea var. minus | 41.6 | 0 | 41.6 | | |
| Oxycoccus quadripetalus | 33.4 | 0 | 33.4 | | |
| (D) Zone : Lagg | | | | 1.527 | 426.7 |
| Group "a" species | | | | | |
| Chamaedaphne calyculata | 96.5 | 43.4 | 54.6 | | |
| Calamagrostis canadensis | 48.3 | 43.5 | 27.3 | | |
| Carex rostrata | 116.0 | 16.3 | 97.1 | | |
| Group "b" species | | | | | |
| Salix bebbiana | 135.8 | 28.3 | 97.4 | | |
| Salix serissima | 4.3 | 28.3(?) | 3.1 | | |

litter fell annually in the Lagg zone, this amount, 524.8 gm./m.$^2$, being between two and three times greater than the amount falling in any of the other three zones. Yet, when the amount of annual litter fall was compared with the value of aerial production, the Bog and Muskeg zones had the greatest annual rate of incorporation. Litter production in all zones amounted to at least 48% of the aerial net production value. Reiner and Reiner (1970, p. 514) had previously found the proportion of above ground net primary production entering the detritus pathway as litter fall to be greater than one half - 51% in a swamp, 55% in an oak forest, and 64% in a fen. The latter value is greater than the 55% recorded for the marginal fen in this study.

TABLE XXIII

TOTAL ANNUAL CONTRIBUTION OF AERIAL VASCULAR PORTIONS TO THE PEATLAND'S SURFACE

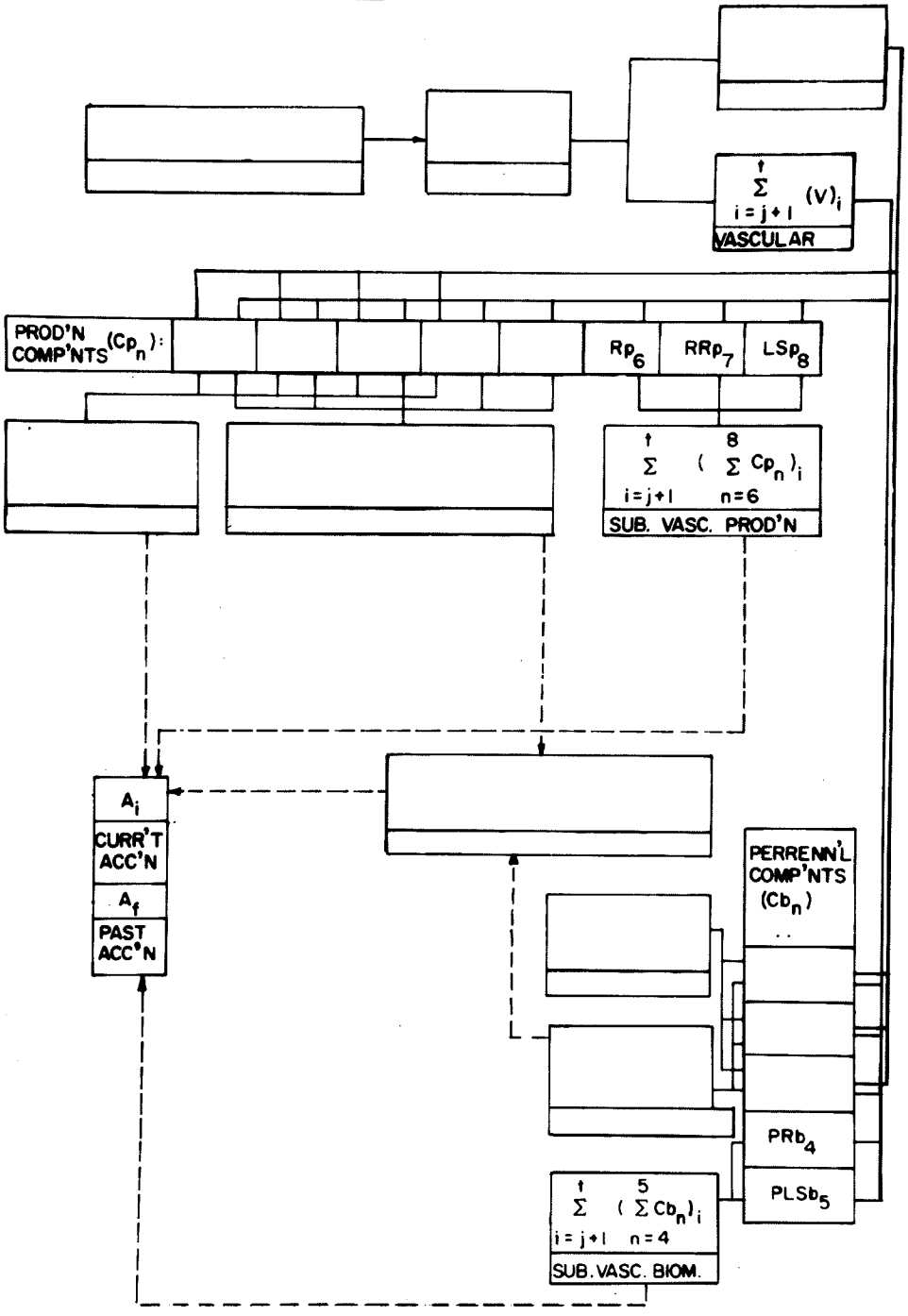
| Zone | (a) gm./m.$^2$ | (b) | (a)(b) = (c) gm./m.$^2$ | % of Current Aerial Net Primary Production |
|---|---|---|---|---|
| Bog Forest | 145.5 | 1.23 | 178.9 | 48.8 |
| Muskeg | 183.8 | 1.23 | 226.1 | 69.4 |
| Bog | 174.8 | 1.23 | 215.0 | 67.9 |
| Lagg | 426.7 | 1.23 | 524.8 | 55.2 |

(a) = $\sum_{i=j+1}^{t} (Lp_1' + FFp_3')_i$ , total leaf and flower-fruit litter weight for important species

(b) = correction factor for other litter types (100/81 = 1.23)

(c) = $\sum_{i=j+1}^{t} [(\sum_{n=1}^{3} Cb_n') + (\sum_{n=1}^{5} Cp_n')]_i$ , TOTAL VASCULAR LITTER

D. 7. Production, biomass, and accumulation of subsurface components of vascular species



In a peatland there is a continuous development of new roots as aerial stems become buried under accumulating peat (Heath et al, 1938, p. 348). Because these roots represent a source of direct addition to peat it was necessary to estimate their biomass and production values. Unfortunately, the difficulty encountered in sampling subsurface portions made it impossible to calculate net production for individual components $Cp_6$ through $Cp_8$ on a species basis. Instead, subsurface net primary production in each zone was estimated (Table XXIV) on the assumption that:

$$\frac{\text{maximum aerial net production}}{\text{average aerial biomass}} = \frac{\text{maximum subsurface net production}}{\text{average subsurface biomass}}$$

Although this equation has not been experimentally verified (Newbould, 1968, p. 188), no other suitable method exists for the estimation of root production.

Values for aerial production and biomass in the above equation were derived previously, while subsurface biomass values were obtained by sampling two 25x25x25 cm. blocks of peat from each of the four zones. The above sampling was carried out at a single date in both July and September to allow for the possible translocation of reserve materials between aerial and subsurface portions (Mooney and Billings, 1960, p. 597; Dahlman and Kucera, 1968, p. 1201). Due to this limited sampling of sub-

surface plant components, biomass values are only approximate.

Most information concerning the relative magnitude of root production has been derived through the use of the so called "root/shoot" ratio, which in this case is mean subsurface biomass divided by mean aerial biomass. Although the usual range of values observed in forested areas is 0.2 - 0.3 (Whittaker and Woodwell, 1968, p. 11), values for the Bog Forest and Lagg zones were approximately 0.5, with figures for the other two zones both greater than unity (Table XXIV). Root/shoot ratios with values between three and eight have previously been reported by Chapman (1970, p. 447) for ericaceous shrubs in a dry heath ecosystem in southern England.

Values of subsurface/aerial production ratios were similar to biomass ratios, with the greatest absolute value of root production, 1461.1 gm./m.$^2$, found in the Bog zone.

The observation that zonal root/shoot ratios increased with greater light exposure, although originally applied to individuals of a single species (Maggs, 1960, p. 434), was also relevant in the current situation. As competition for light increases among species it can be expected that a greater percentage of the total biomass and production will be aerial, with less emphasis placed on subsurface absorbing and supporting organs. Therefore, it was not surprising to find that the

TABLE XXIV

THE TOTAL SUBSURFACE PRODUCTION IN VASCULAR SPECIES FOUND IN EACH OF THE FOUR VEGETATION ZONES

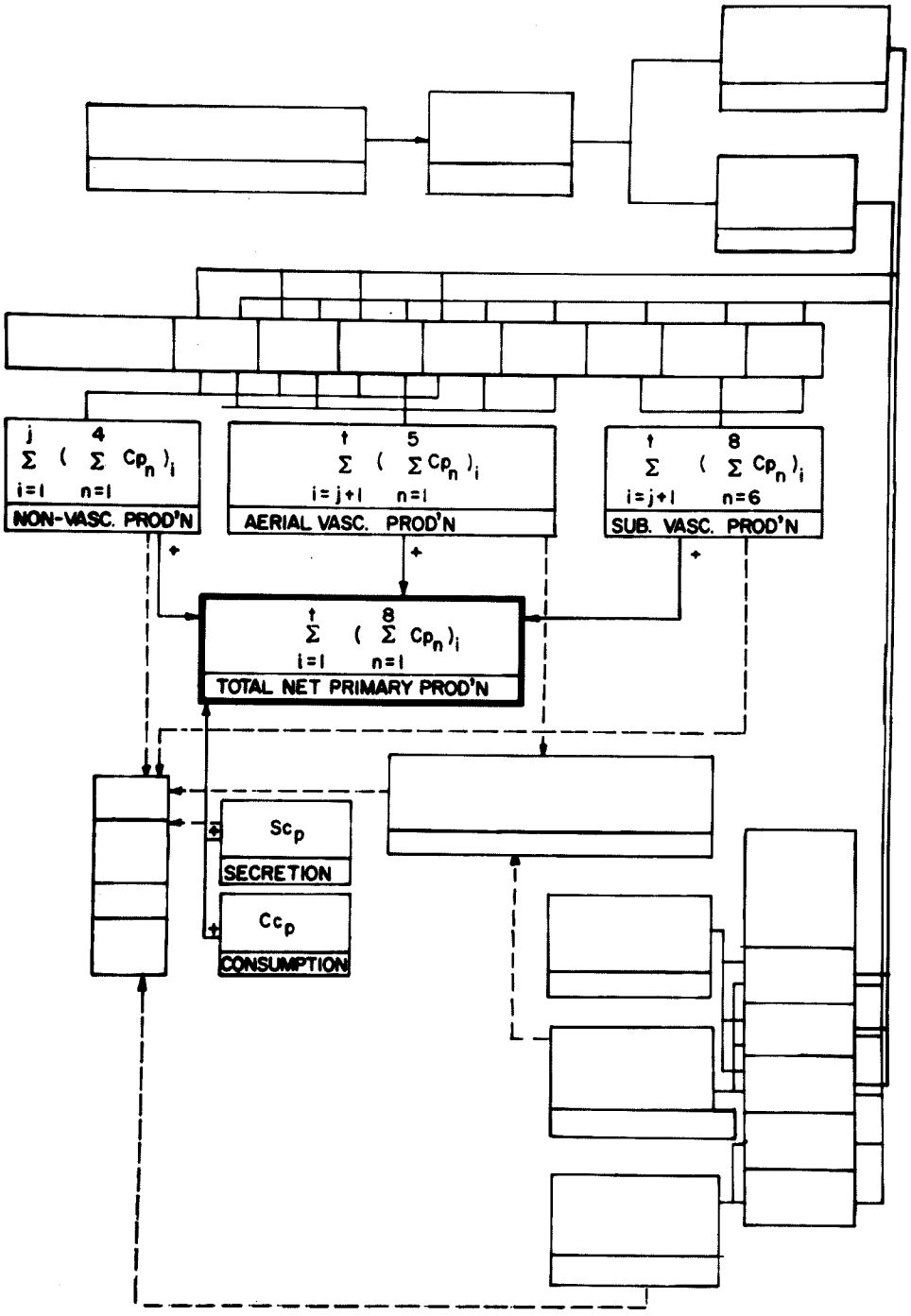
| Zone | Mean Subsurface Biomass gm./m.$^2$ | Maximum aerial production / Mean aerial biomass gm./m.$^2$ | SUB. VASC. PROD'N gm./m.$^2$ | Mean subsurface biomass / Mean aerial biomass |
|---|---|---|---|---|
| Bog Forest | 2280.0 | 366.5/4454.4 | 186.9 | 0.51 |
| Muskeg | 1644.0 | 325.7/901.3 | 593.5 | 1.82 |
| Bog | 1956.0 | 316.4/423.3 | 1461.1 | 4.62 |
| Lagg | 1304.0 | 950.4/2418.8 | 512.5 | 0.54 |

$$\text{SUB. VASC. PROD'N} = \sum_{i=j+1}^{t} \left( \sum_{n=6}^{8} Cp_n \right)_i$$

three treed zones each had greater aerial biomass values than the treeless bog zone, while subsurface biomass values were of similar magnitude in the four zones.

There was no way of estimating the fraction of current subsurface production and perennial biomass added to the detritus cycle annually. Therefore the value calculated for subsurface net production was considered to be equal in magnitude to the actual amount of subsurface "litter" accumulated annually. This was a valid estimate of accumulation income, since the net production total represents the annual addition made by subsurface plant components to existing peat reserves.

E. Total net primary production in each of the four vegetation zones



Total net primary production was calculated as the sum of non-vascular, aerial vascular, and subsurface vascular production. However, the weight of dry matter produced in the current growing season, but lost from plants either through herbivore consumption ($Cc_p$), or by secretion ($Sc_p$), e.g., root exudates and rainwater leaching, was not included in the above total. Consequently, the magnitude of these losses had to be estimated from existing literature values.

The amount of annual leaf consumption found by Crossley (1963, p. 429), Bray (1961, p. 73), and Bray and Gorham (1964, p. 144) approximated 5% to 8% of plant biomass. Based on the small amount of insect damage observed in ericoid leaves (personal observation), and the fact that moss consumption was negligible (Smirnov, 1958, p. 365; 1961, p. 180) it was expected that 5% would represent the maximum percentage lost through consumption.

A small amount of mineral matter is also lost from aerial plant surfaces through rainwater leaching (Tamm, 1951, p. 184; Rodin and Basilevich, 1965, p. 99; Carlisle, Brown and White, 1966, p. 97). The counterpart of such weight loss in subsurface portions is root exudates (Stenlid, 1958, p. 630; Bonner, 1960, p. 396; Woods, 1960). However, it was expected that both of the above exudate losses did not amount to any more than 1%

of the total calculated net primary production.

Therefore, to account for the unmeasured losses of consumption (5%) and secretion (1%), total current net primary production was estimated as 106% of the calculated value in each of the four zones (Table XXV).

The treeless bog zone was the most productive of these zones, with an annual dry matter increment of almost 2000 gm./m.$^2$. This value was much greater than the 300 - 600 gm./m.$^2$ suggested by Rodin and Bazilevich (1965, p. 50) for moss bogs in the U.S.S.R. It was also greater than the maximum value of 420 gm./m.$^2$ reported by Gore and Olson (1967, p. 311) for a high level blanket peatland in England. Most other literature values for peatland production refer only to above ground components (Barclay - Estrup, 1970, p. 246; P'Yavchenko, 1960, p. 597; Solonevich, 1963) in which net production ranged from 178 to 670 gm./m.$^2$. With the exception of the Lagg zone, aerial totals calculated in the current study also fell in this range. It is possible that subsurface production was overestimated in the current study, since the method of determination was based on the yet unverified assumption that the rates of turnover are the same for above and below ground plant components.

TABLE XXV

TOTAL NET PRIMARY PRODUCTION, INCLUDING CORRECTION FOR UNMEASURED LOSSES

| Zone | (a) gm./m.$^2$ | (b) gm./m.$^2$ | (c) gm./m.$^2$ | (d) | [(a)+(b)+(c)](d) = (e) gm./m.$^2$ |
|---|---|---|---|---|---|
| Bog Forest | 116.3 | 366.5 | 186.9 | 1.06 | 709.9 |
| Muskeg | 17.0 | 325.7 | 593.5 | 1.06 | 992.6 |
| Bog | 55.4 | 316.4 | 1461.1 | 1.06 | 1942.6 |
| Lagg | 75.8 | 950.4 | 512.5 | 1.06 | 1631.0 |

(a) $\sum_{i=1}^{j} \left( \sum_{n=1}^{4} Cp_n \right)_i$ , NON-VASC. PROD'N

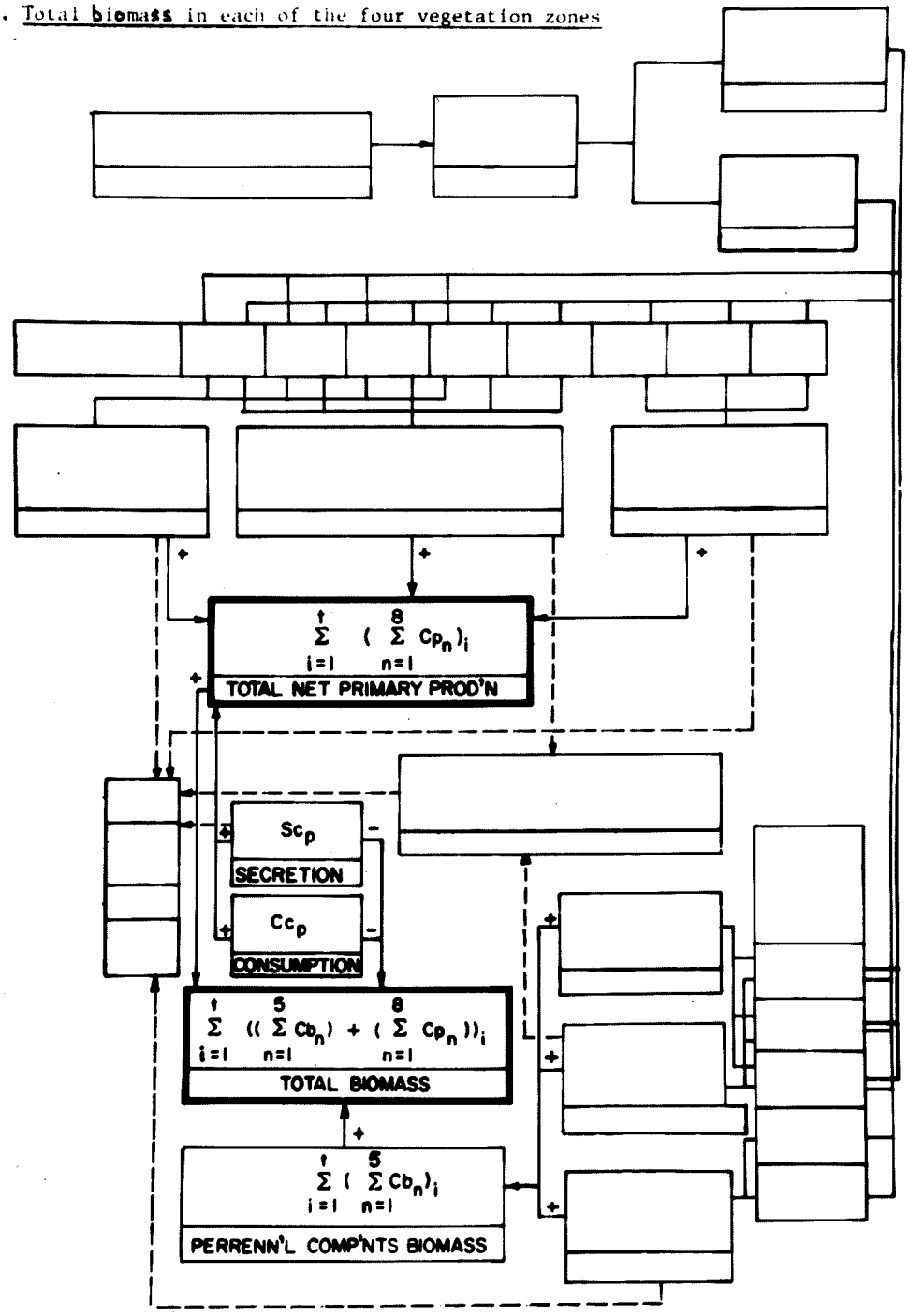
(b) $\sum_{i=j+1}^{t} \left( \sum_{n=1}^{5} Cp_n \right)_i$ , AERIAL VASC. PROD'N

(c) $\sum_{i=j+1}^{t} \left( \sum_{n=6}^{8} Cp_n \right)_i$ , SUB. VASC. PROD'N

(d) = correction for $Sc_p+Cc_p$

(e) $\sum_{i=1}^{t} \left( \sum_{n=1}^{8} Cp_n \right)_i$ , TOTAL NET PRIMARY PROD'N

f. Total biomass in each of the four vegetation zones



Total plant biomass was calculated as the sum of net production and perennial biomass values (Table XXVI). These total biomass values declined from the Bog Forest zone, through the adjacent Muskeg zone, to the Bog zone beyond. On the other hand, zonal net production values showed exactly the opposite trend, i.e., Bog > Muskeg > Bog Forest. Since community stability has been observed to increase with either a decrease in productivity or an increase in biomass (Leigh, 1965, p. 777), then this suggested that of the community types examined, the Bog Forest zone would be least susceptible to change.

A similar conclusion was reached from examining calculated values of the net production/biomass ratio (Table XXVI). As succession proceeds the ratio expressed by primary production/total biomass will drop due to an increase in the biomass and a reduction in the primary production (Margalef, 1963, p. 360). The calculated P/B values suggested the successional sequence to be Bog -> Muskeg -> Bog Forest, which agreed with the scheme previously proposed by Moss (1953a, p. 222). While the P/B value calculated for the Lagg zone (0.428) indicated that it followed the bog stage in the peatland sere, in the present situation it was thought that Bog vegetation replaced Lagg vegetation as peat accumulated and bog vegetation spread into surrounding areas. The replacement of lagg-type vegetation by bog species has prev-

iously been suggested by Cooper (1913, p. 203). Therefore, the course of secondary succession occurring in the study area was considered to be Lagg -> Bog -> Muskeg -> Bog Forest.

TABLE XXVI

TOTAL PLANT BIOMASS IN EACH OF THE FOUR ZONES

| Zone | (a) gm./m.$^2$ | (b) gm./m.$^2$ | (c) gm./m.$^2$ | (a)+(b)+(c) = (d) gm./m.$^2$ | P/B |
|---|---|---|---|---|---|
| Bog Forest | 200.0 | 4454.4 | 2280.0 | 6934.4 | 0.102 |
| Muskeg | 93.7 | 901.3 | 1644.0 | 2639.0 | 0.378 |
| Bog | 131.3 | 423.3 | 1956.0 | 2510.6 | 0.774 |
| Lagg | 87.5 | 2418.8 | 1304.0 | 3810.3 | 0.428 |

(a) $\sum_{i=1}^{j} [(\sum_{n=1}^{4} Cp_n) + (\sum_{n=1}^{3} Cb_n)]_i$ , non-vascular biomass

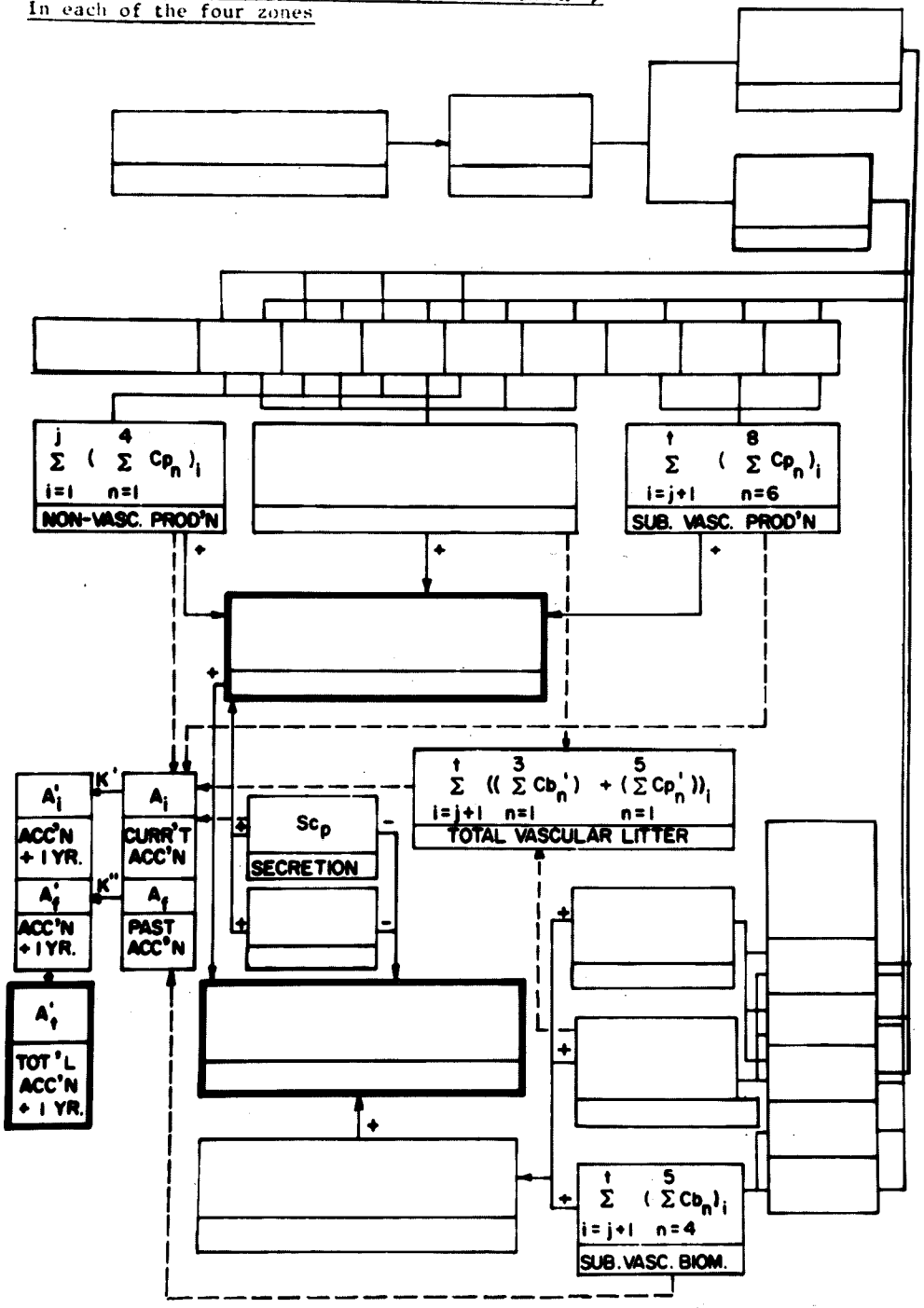
(b) $\sum_{i=j+1}^{t} [(\sum_{n=1}^{5} Cp_n) + (\sum_{n=1}^{3} Cb_n)]_i$ , aerial vascular biomass

(c) $\sum_{i=j+1}^{t} [(\sum_{n=6}^{8} Cp_n) + (\sum_{n=4}^{5} Cb_n)]_i$ , subsurface vascular biomass

(d) $\sum_{i=1}^{t} [(\sum_{n=1}^{8} Cp_n) + (\sum_{n=1}^{5} Cb_n)]_i$ , total plant biomass

P/B = ratio of net primary production to total biomass

G. Estimating the amount of peat accumulated annually in each of the four zones



As indicated in the introduction, values for both the surface accumulation rate of peat, ΔA 1970-71, and $\Delta A_t$, the average amount of peat accumulated annually, were estimated for each of the four vegetation types.

Values of $\Delta A_t$ were previously calculated (p. 33) from measured heights and weights of radiocarbon-dated peat. They represented an estimate of the average amount of peat formed annually by plant types found in the dated cores.

The annual rate of surface accumulation for a number of these same plant types was calculated from empirical values derived for each of the terms in the following accumulation equation:

$$\Delta A_{1970-71} = A'_i = A_i - K'(A_i)$$

1. Calculating accumulation "income"

At this point, consideration has been given to all conceivable sources of accumulation income. The sum of these values provided an estimate of $A_i$, which is the initial weight of peat-forming material added to the peatland's surface annually (Table XXVII).

Of the four zones examined, it was not surprising to find that the Bog zone showed the greatest annual accumulation of litter, 1750 gm./m.$^2$, since this zone also had the greatest net primary production. In the other three zones, the amount of

annual litter was substantially less, i.e., 489-1129 gm./m.$^2$. In these zones more of the net primary production was associated with woody tissues, which were not added to the surface on a yearly basis.

TABLE XXVII

INITIAL WEIGHT OF PEAT-FORMING MATERIAL ADDED ANNUALLY TO THE PEATLAND'S SURFACE

| Zone | (a) gm./m.$^2$ | (b) gm./m.$^2$ | (c) gm./m.$^2$ | (d) $Sc_p$ gm./m.$^2$ | (a)+(b)+(c)+(d) $A_i$ gm./m.$^2$ | $A_i$ as a % of Net Primary Production |
|---|---|---|---|---|---|---|
| Bog Forest | 116.3 | 178.9 | 186.9 | 6.7 | 488.8 | 68.9 |
| Muskeg | 17.0 | 226.1 | 593.5 | 9.4 | 846.0 | 85.2 |
| Bog | 55.4 | 215.0 | 1461.1 | 18.3 | 1749.8 | 90.1 |
| Lagg | 75.8 | 524.8 | 512.5 | 15.4 | 1128.5 | 69.2 |

(a) $\sum_{i=1}^{j} \left( \sum_{n=1}^{4} Cp_n \right)_i$ , NON-VASC. PROD'N

(b) $\sum_{i=j+1}^{t} \left[ \left( \sum_{n=1}^{5} Cp_n' \right) + \left( \sum_{n=1}^{3} Cb_n' \right) \right]_i$ , TOTAL VASCULAR LITTER

(c) $\sum_{i=j+1}^{t} \left( \sum_{n=6}^{8} Cp_n \right)_i$ , SUB. VASC. PROD'N

$A_i$ = CURR'T ACC'N

2. Calculating accumulation "loss"

The decomposition rate ($K'$) of vascular and non-vascular litter components was estimated by enclosing leaf litter in recoverable nylon mesh bags and determining the weight loss after one year.

Observed decomposition rates depended on a number of factors. These included the amount, condition, and placement of enclosed material, as well as the type of enclosure employed.

1. The type of enclosure used: The confinement of litter in mesh bags has raised the question of whether or not observed decomposition rates are natural. Effects of confinement on litter breakdown have been examined by several authors, Witkamp and Olson (1963, p. 146) finding that leaf confinement led to a two to three times slower rate of decomposition, while Woodwell and Marples (1968, p. 462) concluded that confinement had no serious effect on the natural rate of decomposition. Bocock (1964, p. 278) has suggested that the effect of confinement depends on environmental conditions with effects being less marked on "acidic" as opposed to "basic" sites.

The effects of confinement were considered to be minimal in this study.

Gilbert and Bocock (1962, p. 348) reviewed the literature concerning the types of enclosures commonly employed in

decomposition studies, and concluded that mesh bags were the most convenient to use. The mesh size employed regulates the type of decomposer agents entering. Considering that microorganisms represent the chief source of decomposer action in peatlands (Dubos, 1928, p. 26; Clymo, 1965, p. 754), then the use of 1 mm. mesh nylon bags should have had little effect on the natural rate of decomposition (Edwards and Heath, 1963, p. 77). This 1 mm. size was small enough to prevent the loss of material through fragmentation.

2. Amount of material enclosed: Using mesh bags 10x30 cm. for vascular species, and 5x10 cm. for bryophytes, an effort was made to enclose an amount of leaves which would result in a normal spatial distribution when replaced on the peatland's surface. The number was standardized at one hundred for each of the vascular species, with the exception of Carex rostrata, for which only ten leaves and two sheaths were employed. Non-vascular bags contained the green biomass portion of one hundred plants, minus the apices, which ordinarily do not undergo decomposition.

3. Condition of the material subjected to decomposition: Newly fallen leaves and green bryophyte portions were collected in all four vegetation zones at the end of September (1969), and returned to the laboratory for preparation of the decomposition

bags. Since both air and oven drying reduces the amount of natural decomposition (Wollny, 1897, as cited in Starkey, 1924, p. 295; Clymo, 1965, Table VI), the litter was stored in a cold room (6°C.) until replaced on the peatland site seven days later.

A portion of the leaves and mosses collected was oven-dried (105°C.) just before the litter bags were replaced on the peatland's surface. Using the percentage weight loss recorded in this portion, the oven-dry weight of litter replaced on the site was estimated.

4. Placement of the decomposition bags: Two bags per species per zone were placed at an arbitrary position in the zone from which the litter was collected. Leaf portions were placed directly in contact with the moss layer, and in all cases among natural litter of the same species (Figure 15). Moss decomposition bags were placed 0-5 cm. below the surface. This initial placement was completed during the first week of October, 1969.

In October, 1970, the bags were retrieved, returned to the laboratory, contents oven-dried at 105°C., and weights determined. The initial decomposition rate in each species (Table XXVIII) was calculated according to the following formula:

Figure 15. Nylon mesh bags used to determine the initial decomposition rates of leaves in each of the four vegetation zones.

(a) Litter bag located in the Bog Forest zone, containing leaves of Ledum groenlandicum.

(b) Litter bag containing leaves of Chamaedaphne calyculata in the Muskeg zone.

TABLE XXVIII

FRACTION OF ORIGINAL WEIGHT LOST IN LEAVES SUBJECTED TO DECOMPOSITION FOR ONE YEAR

| | Bog Forest | Muskeg | Bog | Lagg |
|---|---|---|---|---|
| | $K'$ | $K'$ | $K'$ | $K'$ |
| (A) Vascular species | | | | |
| Group "a" species | | | | |
| Ledum groenlandicum | 0.332 | 0.178 | 0.138 | |
| Chamaedaphne calyculata | | 0.285 | 0.301 | 0.176 |
| Kalmia polifolia | | 0.142 | 0.355 | |
| Vaccinium vitis-idaea var. minus | | 0.343 | 0.387 | |
| Oxycoccus quadripetalus | | | 0.071 | |
| Carex rostrata | | | | 0.220 |
| Calamagrostis canadensis | | | | - |
| Group "b" species | | | | |
| Picea mariana | 0.243 | 0.337 | | |
| Salix bebbiana | | | | 0.290 |
| Salix serissima | | | | 0.261 |
| (B) Non-vascular species | | | | |
| Pleurozium schreberi | 0.247 | | | |
| Sphagnum fuscum | | 0.017 | 0.001 | |
| Polytrichum juniperinum var. gracilius | | | 0.139 | |
| Aulacomnium palustre | | | 0.089 | 0.076 |
| Hypnum pratense | | | | - |

$K'$ = decomposition rate

$$X = X_o\ (1-K')^t \text{ or } K' = \frac{X_o - X}{X_o} \text{ when } t = 1$$

where X = final litter weight after time t

$X_o$ = initial litter weight

$K'$ = linear decomposition rate between time zero and time t.

The rate of initial weight loss in vascular leaves, 14% - 38%, was greater than the 5% - 15% observed both by Cormack and Gimingham (1964, p. 245) and Chapman (1967, p. 680) in a dry Calluna heath. For non-vascular species, the observed decomposition rate of Pleurozium schreberi, 24.7%, agreed well with the 25.5% loss reported by Mikola (1954), as cited in Kilbertus (1968, p. 22), for the same species. Decomposition weight losses in other non-vascular species were quite small, with a negligible amount, 0.1% - 1.7%, lost in Sphagnum fuscum. While Clymo (1965, p. 749 - 752) has reported losses of up to 20% in several other species of Sphagnum, the small amount of decomposition observed in the current study was not restricted just to S. fuscum. The corresponding range of decomposition values for Sphagnum magellanicum, also found in the Bog zone, was 0 - 3.4%, with 0% decomposition found in bags containing Sphagnum capillaceum.

Thus, while a small amount of non-vascular material was originally accumulated as litter, the percentage of this bryo-

phyte material remaining after one year, and presumably in subsequent years as well, was much greater than in vascular species. While the total amount of peat-forming material initially has a low bryophyte content, the relative importance of this component can be expected to increase over the years, as evidenced by the composition of older peat.

3. Calculating initial accumulation

The value of a species' initial decomposition rate ($K'$) was multiplied by its corresponding litter value ($A_i$) to provide an estimate of the weight lost during the first year of decomposition. The sum of these products was subtracted from the zonal litter value to give the annual surface accumulation rate, $A'_i$. These $A'_i$ values are derived in Tables XXIX - XXXII.

The zonal $A'_i$ values were between twenty and thirty percent less than initial litter values ($A_i$), and decreased in magnitude with succession. This was the result of both an increase in average zonal decomposition values ($K'$), and a corresponding decrease in initial litter values ($A_i$).

Such changes favour the hypothesis that a dynamic equilibrium will be established between "income" and "loss" in the climax situation (Jenny et al, 1949, p. 428).

A further implication of these successional changes is that the theoretical models suggested by Jenny et al (1949), Greeland and Nye (1959), and Olson (1963) to describe the course of organic matter accumulation can not be applied to calculate equilibrium values of peat. Both litter production and initial decomposition rates are assumed to be constant in these models, yet neither appeared to remain fixed in value in the current study. Therefore, equations defining the relation-

TABLE XXIX

WEIGHT OF VASCULAR LITTER REMAINING IN THE FOUR VEGETATION ZONES AFTER ONE YEAR OF DECOMPOSITION

| | (a) $Lp_1' + FFp_3'$ | (b) $K'$ | (a)$_{''}$ - (a)(b) $Lp_1'' + FFp_3''$ | (c) | (d) | $[\sum(a - ab)]$ (c)(d) = (e) |
|---|---|---|---|---|---|---|
| | gm./m.$^2$ | | gm./m.$^2$ | | | gm./m.$^2$ |
| (A) Zone : Bog Forest | | | | 1.031 | 1.23 | 128.6 |
| Group "a" species | | | | | | |
| Ledum groenlandicum | 22.4 | 0.332 | 15.0 | | | |
| Group "b" species | | | | | | |
| Picea mariana | 118.7 | 0.243 | 86.3 | | | |
| (B) Zone : Muskeg | | | | 1.087 | 1.23 | 166.9 |
| Group "a" species | | | | | | |
| Ledum groenlandicum | 65.5 | 0.178 | 53.8 | | | |
| Chamaedaphne calyculata | 20.5 | 0.285 | 14.7 | | | |
| Kalmia polifolia | 8.0 | 0.142 | 6.9 | | | |
| Vaccinium vitis-idaea var. minus | 39.9 | 0.343 | 26.2 | | | |
| Group "b" species | | | | | | |
| Picea mariana | 35.1 | 0.337 | 23.2 | | | |

" = following one year of decomposition

(c) = correction factor for other species, i.e., $\frac{\text{aerial prod'n by all vascular species}}{\text{aerial prod'n by important vasc. species}}$

(d) = correction factor to include other litter types

(e) = $\sum_{i=j+1}^{t} [(\sum_{n=1}^{5} Cp_n'') + (\sum_{n=1}^{3} Cb_n'')]_i$ , aerial vascular litter remaining after decomposition

TABLE XXIX (continued)

| | (a) $Lp_1' + FFp_3'$ | (b) $K'$ | (a)$_{n}$ - (a)(b) $Lp_1'' + FFp_3''$ | (c) | (d) | $[\sum(a - ab)]$ (c)(d) = (e) |
|---|---|---|---|---|---|---|
| | gm./m.$^2$ | | gm./m.$^2$ | | | gm./m.$^2$ |
| (C) Zone : Bog | | | | 1.026 | 1.23 | 162.7 |
| Group "a" species | | | | | | |
| Ledum groenlandicum | 41.3 | 0.138 | 35.6 | | | |
| Chamaedaphne calyculata | 37.8 | 0.301 | 26.4 | | | |
| Kalmia polifolia | 16.3 | 0.355 | 10.5 | | | |
| Vaccinium vitis-idaea var. minus | 41.6 | 0.387 | 25.5 | | | |
| Oxycoccus quadripetalus | 33.4 | 0.071 | 31.0 | | | |
| (D) Zone : Lagg | | | | 1.527 | 1.23 | 400.2 |
| Group "a" species | | | | | | |
| Chamaedaphne calyculata | 54.6 | 0.176 | 45.0 | | | |
| Calamagrostis canadensis | 27.3 | 0.231 | 21.0 | | | |
| Carex rostrata | 97.1 | 0.220 | 75.7 | | | |
| Group "b" species | | | | | | |
| Salix bebbiana | 97.4 | 0.290 | 69.1 | | | |
| Salix serissima | 3.1 | 0.261 | 2.3 | | | |

TABLE XXX

WEIGHT OF SUBSURFACE "LITTER" REMAINING IN THE FOUR VEGETATION ZONES AFTER ONE YEAR OF DECOMPOSITION

| Zone | (a) gm./m.$^2$ | (b) Mean Zonal K' ± One Standard Error % | (a) - (a)(b) = (c) gm./m.$^2$ |
|---|---|---|---|
| Bog Forest | 186.9 | 0.277 ± 7.7% | 135.1 |
| Muskeg | 593.5 | 0.218 ± 12.7% | 464.1 |
| Bog | 1461.1 | 0.155 ± 21.8% | 1234.6 |
| Lagg | 512.5 | 0.231 ± 11.6% | 394.1 |

" = following one year of decomposition

(a) $\sum_{i=j+1}^{t} \left( \sum_{n=6}^{8} Cp_n \right)_i$ , SUB. VASC. PROD'N

(c) $\sum_{i=j+1}^{t} \left( \sum_{n=6}^{8} Cp_n'' \right)_i$ , subsurface vascular "litter" remaining after decomposition

TABLE XXXI

WEIGHT OF NON-VASCULAR LITTER REMAINING AFTER ONE YEAR OF DECOMPOSITION

| | (a) | (b) | (a) - (a)(b) | (c) | $[\sum(a - ab)](c) = (d)$ |
|---|---|---|---|---|---|
| | gm./m.$^2$ | | gm./m.$^2$ | | gm./m.$^2$ |
| (A) Zone : Bog Forest | | | | 1.08 | 87.6 |
| *Pleurozium schreberi* | 107.7 | 0.247 | 81.1 | | |
| (B) Zone : Muskeg | | | | 2.39 | 16.7 |
| *Sphagnum fuscum* | 7.1 | 0.017 | 7.0 | | |
| (C) Zone : Bog | | | | 1.15 | 49.3 |
| *Sphagnum fuscum* | 7.8 | 0.001 | 7.8 | | |
| *Polytrichum juniperinum* var. *gracilius* | 35.0 | 0.139 | 30.1 | | |
| *Aulacomnium palustre* | 5.4 | 0.089 | 5.0 | | |
| (D) Zone : Lagg | | | | 1.13 | 64.6 |
| *Aulacomnium palustre* | 35.9 | 0.076 | 33.2 | | |
| *Hypnum pratense* | 31.2 | 0.231 | 24.0 | | |

(a) = $\sum_{n=1}^{4} Cp_n$ , annual litter

(b) = K' , decomposition rate

(a) - (a)(b) = $\sum_{n=1}^{4} Cp''_n$ , litter after decomposition

(c) = correction factor for "other" species, i.e., $\frac{\text{total cover \% by all species}}{\text{total cover \% by important species}}$

(d) = $\sum_{i=1}^{j} \left( \sum_{n=1}^{4} Cp''_n \right)_i$ , total non-vascular litter following decomposition

TABLE XXXII

TOTAL WEIGHT OF LITTER REMAINING AFTER ONE YEAR OF DECOMPOSITION

| Zone | (a) gm./m.$^2$ | (b) gm./m.$^2$ | (c) gm./m.$^2$ | (d) gm./m.$^2$ | (a)+(b)+(c)-(d) $A_i'$ gm./m.$^2$ | $A_i' / A_i$ | $A_i'$ / Total Net Primary Production |
|---|---|---|---|---|---|---|---|
| Bog Forest | 87.6 | 128.6 | 135.1 | 6.7 | 344.6 | 0.705 | 0.485 |
| Muskeg | 16.7 | 166.9 | 464.1 | 9.4 | 638.3 | 0.754 | 0.643 |
| Bog | 49.3 | 162.7 | 1234.6 | 18.3 | 1428.3 | 0.816 | 0.735 |
| Lagg | 64.6 | 400.2 | 394.1 | 15.4 | 843.5 | 0.747 | 0.517 |

(a) $\sum_{i=1}^{j} \left( \sum_{n=1}^{4} Cp_n'' \right)_i$ , total non-vascular litter following decomposition

(b) $\sum_{i=j+1}^{t} \left[ \left( \sum_{n=1}^{5} Cp_n'' \right) + \left( \sum_{n=1}^{3} Cb_n'' \right) \right]_i$ , aerial vascular litter remaining after decomposition

(c) $\sum_{i=j+1}^{t} \left( \sum_{n=6}^{8} Cp_n'' \right)_i$ , subsurface vascular "litter" remaining after decomposition

(d) = 1% of $\sum_{i=1}^{t} \left( \sum_{n=1}^{8} Cp_n \right)_i = Sc_{p,b}$

$A_i'$ = total weight of litter remaining after one year of decomposition

ship of both litter production and initial decomposition rate with time must be established. In the present study, an attempt was made to derive such equations by plotting observed zonal litter and decomposition values against the maximum radiocarbon age of each zone. Unfortunately however, previous surface fires in the area had altered surface vegetation types such that it was impossible to derive a logical relationship between total peat depth, present surface vegetation type, and time, in the four zones. Only in a situation where unidirectional succession has occurred can these relationships be quantified for use in the above models.

To determine the relationship between surface accumulation and current net primary production a "surface accumulation ratio" was established, i.e., the zonal $A'_i$ value divided by zonal net primary production. Table XXXII indicated that following an initial year of decomposition, at least 0.48 of the original net primary production total still remained, with this fraction having a maximum value of 0.74 in the Bog zone.

Since decomposition had not been completed during this first year, then $A'_i$ values did not indicate the amount of original production which would eventually remain as inert peat. The value of this undecomposed fraction could not be calculated directly. However, $\Delta A_t$ values represented a rough estimate of

this annual accumulation rate. Derived by radiocarbon dating existing peat reserves, the range of these values, 26.8 - 51.7 $gm./m.^2$, was considered to be a slight underestimate of the true accumulation rate, due to the past occurrence of surface fires in the area. Yet, estimates of even twice this range would still amount to less than one fifth the amount of original production in any zone. Thus, the percentage of original net primary production which is eventually stored as inert peat is small indeed.

A concise summary of the important successional changes occurring during the accumulation process, represented in this case by income, loss, and net accumulation terms, is provided in Table XXXIII.

In addition, a visual summary of the distribution scheme for plant matter resulting from net primary production is found in Figure 16. This is simply the original scheme now having numerical values attached to each of the component blocks[1]. Direct comparison of successional changes in any of the calculated values can easily be made using these figures.

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[1] Not knowing the fraction of litter remaining undecomposed, it was impossible to calculate values for $K''$, $A'_f$ and $A'_t$.

TABLE XXXIII

SUMMARY OF SUCCESSIONAL CHANGES IN NET PRIMARY PRODUCTION AND ACCUMULATION

| Attribute | Lagg | Bog | Muskeg | Bog Forest |
|---|---|---|---|---|
| (A) Accumulation income | | | | |
| Total annual net primary production (gm./m.$^2$) | 1631.0 | 1942.9 | 992.6 | 709.9 |
| Percentage of aerial production in non-vascular species | 7.4 | 14.9 | 5.0 | 24.1 |
| Percentage of aerial production in vascular species | 92.6 | 85.1 | 95.0 | 75.9 |
| Vascular "Root/Shoot" ratio | 0.54 | 4.62 | 1.82 | 0.51 |
| Percentage of total net primary production added annually as peat-forming material | 69.2 | 90.1 | 85.2 | 68.9 |
| Total net primary production/total biomass, i.e., P/B | 0.428 | 0.774 | 0.378 | 0.102 |
| (B) Accumulation loss | | | | |
| Mean zonal decomposition rate during the initial year of decomposition | 0.231 | 0.155 | 0.218 | 0.277 |
| (C) Net accumulation | | | | |
| Length of accumulation period (years) | 2960. | - | 7939. | 4524. |
| Present peat depth (cm.) | 57.5 | 106.5 | 206.5 | 166.0 |
| Present peat weight (gm./m.$^2$) | 106455.5 | 105498.9 | 229710.6 | 145565.4 |
| $\Delta A_{1970-1971}$ (gm./m.$^2$/yr.) | 830.5 | 1423.2 | 632.9 | 336.6 |
| $\Delta A_{1970-1971}$ / Total net primary production | 0.517 | 0.735 | 0.643 | 0.485 |
| $\Delta A_t$ (height) (cm./yr.) | 0.0279 | - | 0.0255 | 0.0414 |
| $\Delta A_t$ (weight) (gm/m.$^2$/yr.) | 51.7 | - | 26.8 | 36.3 |

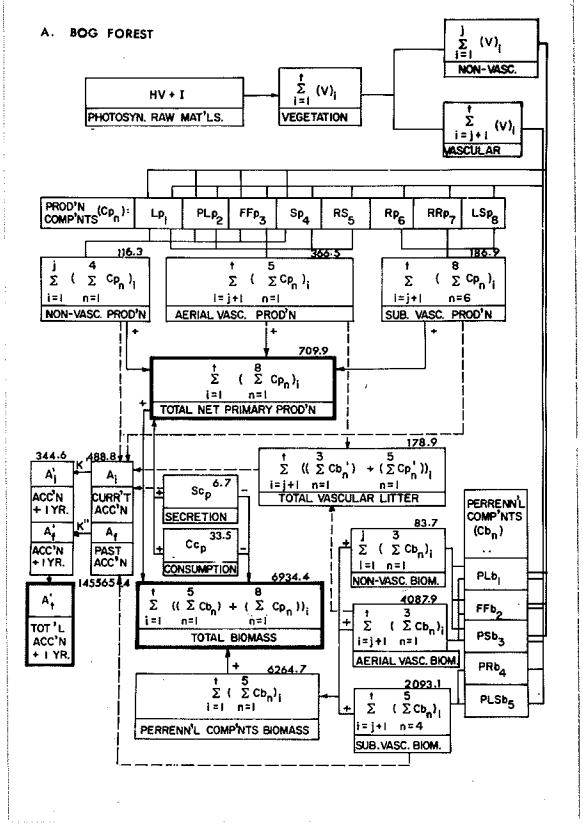
Figure 16. Numerical values for both net primary production and the annual accumulation of peat in each of the four vegetation zones. All numerical values shown are in grams per square meter.

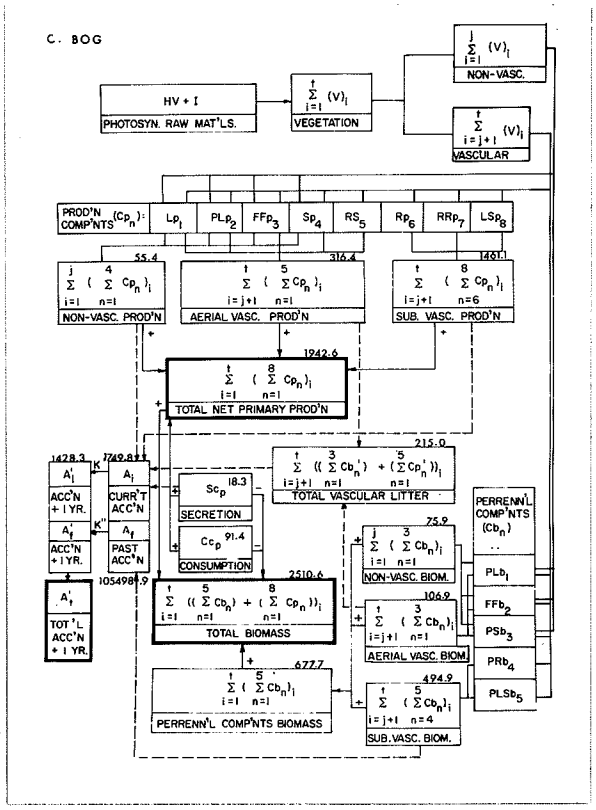
(A) Bog Forest zone

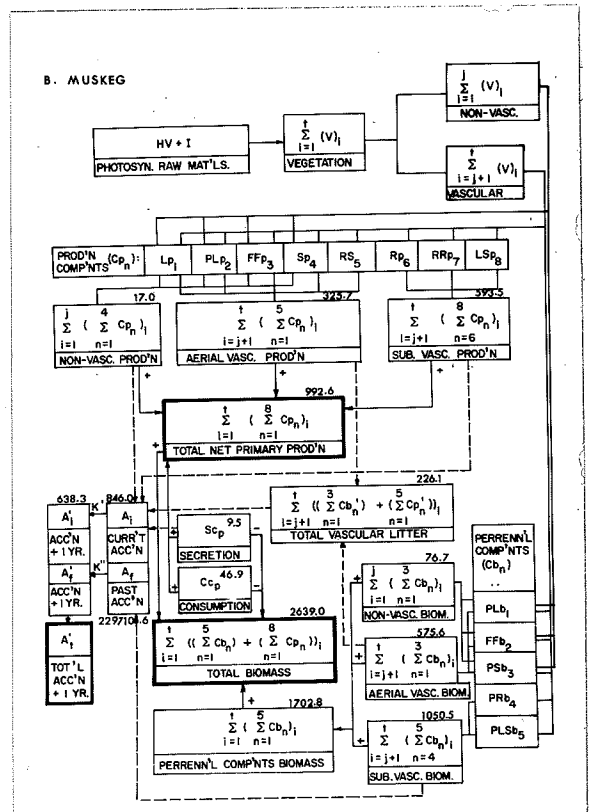
(B) Muskeg zone

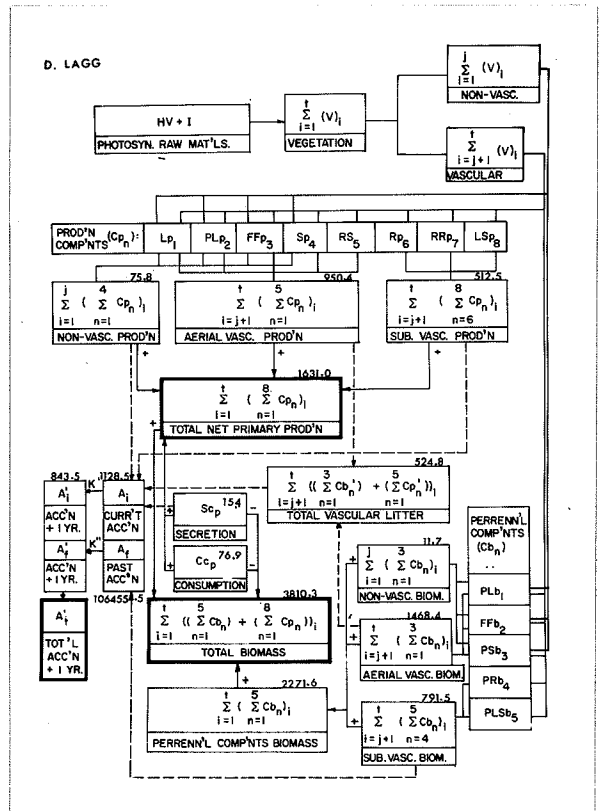
(C) Bog zone

(D) Lagg zone


A. BOG FOREST
HV + I
PHOTOSYN. RAW MAT'LS.
VEGETATION
NON-VASC.
VASCULAR
PROD'N COMP'NTS (Cp_n):
Lp_1
PLp_2
FFp_3
Sp_4
RS_5
Rp_6
RRp_7
LSp_8
116.3
366.5
186.9
NON-VASC. PROD'N
AERIAL VASC. PROD'N
SUB. VASC. PROD'N
709.9
TOTAL NET PRIMARY PROD'N
344.6
488.8
178.9
ACC'N + 1 YR.
CURR'T ACC'N
PAST ACC'N
TOT'L ACC'N + 1 YR.
Sc_p 6.7
SECRETION
Cc_p 33.5
CONSUMPTION
TOTAL VASCULAR LITTER
PERRENN'L COMP'NTS (Cb_n)
PLb_1
FFb_2
PSb_3
PRb_4
PLSb_5
145365.4
6934.4
TOTAL BIOMASS
83.7
NON-VASC. BIOM.
4087.9
AERIAL VASC. BIOM.
6264.7
PERRENN'L COMP'NTS BIOMASS
2093.1
SUB. VASC. BIOM.


C. BOG
HV + I
PHOTOSYN. RAW MAT'LS.
VEGETATION
NON-VASC.
VASCULAR
PROD'N COMP'NTS (Cp_n):
Lp_1
PLp_2
FFp_3
Sp_4
RS_5
Rp_6
RRp_7
LSp_8
55.4
316.4
1401.1
NON-VASC. PROD'N
AERIAL VASC. PROD'N
SUB. VASC. PROD'N
1942.6
TOTAL NET PRIMARY PROD'N
1428.3
1749.8
215.0
ACC'N + 1 YR.
CURR'T ACC'N
PAST ACC'N
TOT'L ACC'N + 1 YR.
Sc_p 18.3
SECRETION
Cc_p 91.4
CONSUMPTION
TOTAL VASCULAR LITTER
PERRENN'L COMP'NTS (Cb_n)
PLb_1
FFb_2
PSb_3
PRb_4
PLSb_5
1054984.9
2510.6
TOTAL BIOMASS
75.9
NON-VASC. BIOM.
106.9
AERIAL VASC. BIOM.
677.7
PERRENN'L COMP'NTS BIOMASS
494.9
SUB. VASC. BIOM.


B. MUSKEG
HV + I
PHOTOSYN. RAW MAT'LS.
VEGETATION
NON-VASC.
VASCULAR
PROD'N COMP'NTS (Cp_n):
Lp_1
PLp_2
FFp_3
Sp_4
RS_5
Rp_6
RRp_7
LSp_8
17.0
325.7
393.5
NON-VASC. PROD'N
AERIAL VASC. PROD'N
SUB. VASC. PROD'N
992.6
TOTAL NET PRIMARY PROD'N
638.3
846.0
226.1
ACC'N + 1 YR.
CURR'T ACC'N
PAST ACC'N
TOT'L ACC'N + 1 YR.
Sc_p 9.5
SECRETION
Cc_p 46.9
CONSUMPTION
TOTAL VASCULAR LITTER
PERRENN'L COMP'NTS (Cb_n)
PLb_1
FFb_2
PSb_3
PRb_4
PLSb_5
229710.6
2639.0
TOTAL BIOMASS
76.7
NON-VASC. BIOM.
575.6
AERIAL VASC. BIOM.
1702.8
PERRENN'L COMP'NTS BIOMASS
1050.5
SUB. VASC. BIOM.


D. LAGG
HV + I
PHOTOSYN. RAW MAT'LS.
VEGETATION
NON-VASC.
VASCULAR
PROD'N COMP'NTS (Cp_n):
Lp_1
PLp_2
FFp_3
Sp_4
RS_5
Rp_6
RRp_7
LSp_8
75.8
950.4
512.5
NON-VASC. PROD'N
AERIAL VASC. PROD'N
SUB. VASC. PROD'N
1631.0
TOTAL NET PRIMARY PROD'N
843.5
1128.5
524.8
ACC'N + 1 YR.
CURR'T ACC'N
PAST ACC'N
TOT'L ACC'N + 1 YR.
Sc_p 15.4
SECRETION
Cc_p 76.9
CONSUMPTION
TOTAL VASCULAR LITTER
PERRENN'L COMP'NTS (Cb_n)
PLb_1
FFb_2
PSb_3
PRb_4
PLSb_5
1064554.5
3810.3
TOTAL BIOMASS
11.7
NON-VASC. BIOM.
1468.4
AERIAL VASC. BIOM.
2271.6
PERRENN'L COMP'NTS BIOMASS
791.5
SUB. VASC. BIOM.

# Chapter IV

## SUMMARY AND CONCLUSIONS

In the preceeding pages an effort has been made to answer the two basic questions posed in the introduction, i.e., what is the net primary production of peatland vegetation, and what fraction of production is subsequently accumulated annually as peat?

In the present study both questions were asked of four peatland vegetation types - a marginal lagg, a treeless bog, a muskeg, and a bog forest. All were found in close proximity, and represented different seral stages in the process of peatland succession in southern Manitoba. This added another dimension to the problem, with the aim of the current study being to establish numerical relationships between peatland production, accumulation and time.

The simple equation "accumulation = income-loss" was first expanded and presented in terms of a block diagram to define all potential sources of both income and loss. Numerical values were attached to each of the blocks in this scheme to solve the accumulation equation in each of the vegetation types examined.

"Income" in this equation resulted from the annual production of dry matter in surface vegetation, its death at the end of the growing season, and subsequent accumulation as "litter".

The annual net primary production of vegetation in each of the four zones was measured on an individual basis. This involved establishing dry weight values for current production in each of the components of individual plants. Time limitations prevented the desired degree of accuracy (standard error of ± 10%) from being achieved in all measurements, e.g., radial stem increments. All species considered to be important contributors to zonal net primary production were studied on an individual basis. "Individual" sampling was carried out at regular intervals through an entire growing season, which allowed maximum production values to be derived for each component, and also allowed the pattern of dry weight increase to be plotted. The majority of species had a sigmoid growth curve. The variation among weekly production values in the upper plateau portion of the curve could be reduced by increasing the number of plants sampled at each date.

The assumption that the relative productivity of a species was related to its frequency was originally used to delimit "important" and "less important" species in each of the four zones. This assumption was verified by comparing species' rankings based on relative frequency and aerial production. Yet, comparison of the absolute net production values of the same species in two or more of the zones examined, indi-

cated that differences existed both in plant density and in individual plant production. These differences suggested the existence of zonal microenvironments.

Such differences also indicated that values of both density and individual plant production must be known before any conclusions can be drawn concerning the production potential of a species.

Total aerial net primary production in each of the four zones was calculated as the product of the sum of important species' production and a correction factor for the production of unmeasured species. This correction was calculated on the assumption that unmeasured species had a production mean equivalent to the average value of those species in which production was actually measured. Aerial production totals were greatest in the heavily treed zones, i.e., Lagg (1026 gm./m.$^2$) and Bog Forest (482 gm./m.$^2$), with smaller totals recorded in the Bog (371 gm./m.$^2$) and Muskeg zones (342 gm./m.$^2$). Since not all measurements were made with the same degree of accuracy, differences in the magnitude of zonal totals was of greater interest than were the absolute values of these net production totals.

While the moss component of vegetation formed almost a continuous layer in the Bog, Muskeg, and Bog Forest zones, up

to 95% of the aerial dry matter produced annually was contributed by vascular species. However, non-vascular production, especially Sphagnum production, may have been underestimated, since some difficulty was encountered in distinguishing between new and old growth.

The net primary production of subsurface components was calculated directly for each zone. Values of the subsurface biomass/aerial biomass ratio were greater than unity in both the Bog and Muskeg zones, indicating a high percentage of total production to be associated with these subsurface portions. The greatest subsurface net production total, 1461.1 gm./m.$^2$ was recorded in the Bog zone, with a minimum of 186.9 gm./m.$^2$ in the Bog Forest. The aerial plus subsurface net primary production total was also maximum in the Bog zone, 1943 gm./m.$^2$, while values of the same total declined through the other three zones to a minimum of 710 gm./m.$^2$ in the Bog Forest. These calculated net production totals were much greater than those previously reported.

The results for aerial production in the current study were comparable to existing literature values. In contrast, values for subsurface production, and consequently for the total of aerial plus subsurface production, were much greater than previous estimates. However, it was suggested that this may

have been partly due to the method of analysis. This indicates the need for a suitable, yet accurate method for the estimation of annual root production for use in future studies.

Combining the above production totals with biomass values to form production/biomass ratios (P/B), allowed some important conclusions to be drawn concerning the direction of secondary succession in the four vegetation types. It has been previously inferred that the amount of biomass supported per unit of production increases with succession to become a maximum in the climax situation (odum, 1969, p. 263; Margalef, 1963, p. 360). If this is the case, then P/B values calculated in the present study indicated a succession of vegetation types proceeding from the Bog, through the Muskeg, to a Bog Forest-type of vegetation, as previously hypothesized by Moss (1953a, p. 222).

While the lower P/B value of the Lagg zone suggested it to be more mature than the Bog zone, in the present situation it was thought that bog vegetation replaced lagg vegetation as peat accumulated and bog vegetation spread into surrounding areas. Therefore, the course of secondary succession occurring in the study area is believed to be Lagg -> Bog -> Muskeg -> Bog Forest.

According to the accumulation scheme, a portion of aerial

net primary production is added to the surface of the peatland at the end of the growing season, while subsurface production is added directly to former peat reserves. Aerial litter amounted to a minimum of 49% of annual net primary production in each of the four zones, while including subsurface litter raised this minimum figure to 69%.

"Loss" in the accumulation process is due primarily to the decomposition of plant litter. The initial decomposition weight loss recorded for vascular leaf litter was greater than the corresponding loss occurring in non-vascular species. Therefore, even though the initial litter contribution made by bryophytes was smaller than that of vascular species, after several years of decomposition non-vascular remains would eventually form the bulk of accumulated peat.

On a zonal basis, approximately one quarter of the original litter was lost during the first year of decomposition, with the average initial decomposition rate increasing with succession, i.e., from the Bog to Bog Forest zones. This favours the hypothesis that in the climax situation "loss" equals "income".

The fact that the average zonal decomposition rate does not remain constant with time is of great importance when considering the possibility of calculating equilibrium accumula-

tion totals from models based on geometric progressions. The models of Jenny et al (1949), Greenland and Nye (1959) and Olson (1963) assume both constant litter production and initial decomposition rates, while neither appeared to remain constant over the successional period in the current study. Unless the function defining the relationship between litter production, initial decomposition rate and time are known, these accumulation models should not be applied. The fact that succession was not unidirectional in the present study prevented the relationship between each of the two variables and time from being established.

The empirically derived values for both "income" and "loss" were used to solve the accumulation equation in each of the four zones. After one year of decomposition the amount of peat-forming material present ranged from a maximum of 1428 gm./m.$^2$ in the Bog zone, to a minimum of 345 gm./m.$^2$ in the Bog Forest. Thus, the relationship between surface accumulation and successional time is similar to that between zonal net primary production and time,

i.e., Bog > Lagg > Muskeg > Bog Forest.

A relationship between annual net primary production and the resulting surface accumulation was derived by dividing the surface accumulation total by the net primary production ob-

served in the same zone. This "surface accumulation ratio" was a maximum in the Bog zone, where almost three quarters of the original net primary production still remained after one year. A minimum value of 0.48 was recorded in the Bog Forest zone.

Since decomposition had not been completed in the litter after one year, then the fraction of initial production eventually accumulated as inert peat would be considerably less.

An approximation of the annual accumulation rate of inert peat was provided by radiocarbon-dating a portion of the peat accumulated during previous years. The range of values indicated by this C-14 dating, 26.8 - 51.7 gm./m.$^2$, represented less than one tenth the value of original production in any of the four zones examined. Reducing the zonal value for material remaining after one year ($A'_i$) by one order of magnitude provides a reasonable estimate of the relative amount accumulated annually by each vegetation type.

Calculation of the actual amount of peat formed by each vegetation type would require an examination of the decomposition process over a number of years. Such an examination would provide values for the decomposition and accumulation rate of peat formed in previous years, i.e., K" and $A'_f$, which were not calculated in the present study. Time limitations prevented

this from being undertaken. Heinselman (1970, p. 259) has recently emphasized the need to also understand the chemical and microbial factors regulating the rate of peat accumulation and decay, for these factors regulate the topographic evolution of surface vegetation types. An investigation of abiotic influences on the rate of accumulation in the four zones is suggested. Thus, while the present study has provided a partial solution to questions concerning the rate and amount of peat accumulation, questions concerning the "how" and "why" of peat accumulation still have to be answered.

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# APPENDICES

A. Species identified in the study area

Voucher specimens of the following species, collected from the peatland near Elma, Manitoba, have been placed in the herbarium of the University of Manitoba. Nomenclature and arrangement of vascular species is according to Scoggan (1957), while that of bryophytes is after Crum et al (1965), and for lichens, Hale and Culberson (1966).

(a) Vascular species

| | |
|---|---|
| Pinaceae | Pinus banksiana Lamb. |
| | Larix laricina (Du Roi) K. Koch |
| | Picea mariana (Mill.) BSP. |
| Gramineae | Calamagrostis canadensis (Michx.) Nutt. |
| Cyperaceae | Eriophorum spissum Fern. |
| | Carex aquatilis Wahl. |
| | Carex canescens L. |
| | Carex rostrata Stokes |
| Liliaceae | Smilacina trifolia (L.) Desf. |
| Salicaceae | Populus balsamifera L. |
| | Populus tremuloides Michx. |
| | Salix bebbiana Sarg. |
| | Salix pedicellaris Pursh. var. hypoglauca Fern. |
| | Salix petiolaris Sm. |

| | |
|---|---|
| Salicaceae | Salix serissima (Bailey) Fern. |
| | Salix pyrifolia Anderss. |
| | Salix discolor Muhl. |
| Betulaceae | Alnus rugosa (Du Roi) Spreng. var. americana (Regel) Fern. |
| | Betula glandulosa Michx. var. glandulifera (Regel) Gl. |
| Saxifragaceae | Ribes hirtellum Michx. |
| Rosaceae | Rubus idaeus L. var. strigosus (Michx.) Maxim. |
| | Rubus acaulis Michx. |
| | Amelanchier alnifolia Nutt. |
| Onagraceae | Epilobium angustifolium L. |
| Cornaceae | Cornus stolonifera Michx. |
| Ericaceae | Ledum groenlandicum Oeder |
| | Chamaedaphne calyculata (L.) Moench |
| | Kalmia polifolia Wang. |
| | Andromeda glaucophylla Link |
| | Gaultheria hispidula (L.) Bigel. |
| | Oxycoccus quadripetalus Gilib. |
| | Vaccinium angustifolium Ait. |
| | Vaccinium myrtilloides Michx. |

| | |
|---|---|
| Ericaceae | *Vaccinium vitis-idaea* L. var. *minus* Lodd. |
| Caprifoliaceae | *Lonicera villosa* (Michx.) R & S var. *solonis* (Eat.) Fern. |
| Compositae | *Petasites sagittatus* (Pursh) Gray |
| | *Petasites vitifolius* Greene |

(b) Non-vascular species

(i) Bryophytes:

| | |
|---|---|
| Sphagnaceae | *Sphagnum capillaceum* (Weiss) Schrank |
| | *Sphagnum fuscum* (Schimp.) Klinggr. |
| | *Sphagnum magellanicum* Brid. |
| | *Sphagnum recurvum* P. Beauv. (*sensu latu*) |
| Dicranaceae | *Dicranum polysetum* Sw. |
| | *Dicranum undulatum* Brid. |
| Aulacomniaceae | *Aulacomnium palustre* (Hedw.) Schwaegr. |
| Thuidiaceae | *Thuidium recognitum* (Hedw.) Lindb. |
| | *Helodium blandowii* (Web. and Mohr) Warnst. |
| Brachytheciaceae | *Tomenthypnum nitens* (Hedw.) Loeske |
| Entodontaceae | *Pleurozium schreberi* (Brid.) Mitt. |
| Hypnaceae | *Hypnum pratense* Koch ex Spruce[1] |

[1] Awaiting verification

| | |
|---|---|
| Hypnaceae | Ptilium crista-castrensis (Hedw.) De Not. |
| Hylocomniaceae | Hylocomium splendens (Hedw.) B.S.G. |
| Polytrichaceae | Polytrichum commune (Hedw.) |
| | Polytrichum juniperinum Hedw. var. gracilius Wahlenb. |

(ii) Lichens

| | |
|---|---|
| Cladoniaceae | Cladonia carneola (Fr.) Fr. |
| | Cladonia cenotea (Ach.) Schaer. |
| | Cladonia cristatella Tuck. |
| | Cladonia gracilia (L.) Wills. var. dilatata (Hoffm.) Vain. |
| | Cladonia mitis Sandst. |
| | Cladonia multiformis Merr. |
| | Cladonia rangiferina Wigg. |

B. Data processing by digital computer

The tremendous number of calculations required to calculate production and accumulation totals in the current study limits the feasibility of applying a similar technique in other situations. The digital computer proved to be a partial solution to this problem.

A computer programme, written in WATFIV to accompany the original scheme (Figure 4), handled the final portion of the data processing involved. Input to Programme 3 consisted of net primary production values ($gm./m.^2$) for components of all important species in each of the vegetation zones studied. When corresponding biomass and litter values were also supplied, the final result was an output of zonal net primary production, biomass and surface accumulation totals, as well as ratios expressing the relationship between annual net production, biomass and accumulation.

Explanatory comments have been inserted liberally throughout the listing of the programme to indicate what calculations are being performed. Symbols employed are those introduced in Figure 4.

Programme 3. Calculating the annual net primary production, biomass, and surface accumulation rate of peatland vegetation according to the scheme presented in Figure 4.

```
C  PROGRAMME 3
C  THIS PROGRAMME IS WRITTEN IN WATFIV FOR THE I.B.M. 360-65
C  IT CALCULATES THE PRODUCTION AND ACCUMULATION OF VEGETATION
C  IN A PEATLAND ECOSYSTEM
C
C  ALL NUMERICAL VALUES ARE IN GRAMS PER SQUARE METER
C
      CHARACTER*80 TITLE
      INTEGER*4 IN/5/,OUT/6/
      LOGICAL*1 OK
      REAL*4 COMP(24,5),CORF(24),BIOM(24),PROD(24),PRODC(24)
      REAL*4 SUBPRD(4),SUBTBL(4)
      REAL*4 SUBDEC(4)
      REAL*4 C2(24),C4(8),C6(24),C8(8),C10(4),C13(4),C15(4),C18(8),
     *       C19(8),C21(8),C23(4),C24(4),C27(8),C29(4),C30(4),C33(4)
     *       C3627(8),C3629(4),C3630(4),C3633(4),C39(4),C25(4)
C
C  EACH IMPORTANT SPECIES IS GIVEN A CODED NUMBER (01-15),
C  WITH SIMILIAR SPECIES HAVING THE SAME CLASS-
C  PERENNIAL AND SEMIDECIDUOUS(B) OR DECIDUOUS(A),
C  THE SAME TYPE-VASCULAR(+) OR NON-VASCULAR(-),
C  AND THE SAME ZONE-BOG FOREST(1),MUSKEG(2),BOG(3),AND LAGG(4).
C  THIS RESULTS IN 24 ZONE-TYPE-CLASS-SPECIES COMBINATIONS
C
C  1+B15  PICEA MARIANA (MILL.) BSP.                    BOG FOREST
C  1+B08  LEDUM GROENLANDICUM OEDER                     BOG FOREST
C  1-B04  PLEUROZIUM SCHREBERI (BRID.)MITT.             BOG FOREST
C  2+B15  PICEA MARIANA (MILL.) BSP.                    MUSKEG
C  2+B08  LEDUM GROENLANDICUM OEDER                     MUSKEG
C  2+B06  CHAMAEDAPHNE CALYCULATA(L.)MOENCH             MUSKEG
C  2+B10  VACCINIUM VITIS-IDAEA L. VAR. MINUS LODD.     MUSKEG
C  2+B07  KALMIA POLIFOLIA WANG.                        MUSKEG
C  2-A05  SPHAGNUM FUSCUM (SCHIMP.) KLINGGR.            MUSKEG
C  3+B06  CHAMAEDAPHNE CALYCULATA(L.)MOENCH             BOG
C  3+B08  LEDUM GROENLANDICUM OEDER                     BOG
C  3+B09  OXYCOCCUS QUADRIPETALUS GILIB.                BOG
C  3+B10  VACCINIUM VITIS-IDAEA L. VAR. MINUS LODD.     BOG
C  3+B07  KALMIA POLIFOLIA WANG.                        BOG
C  3-B01  AULACOMNIUM PALUSTRE(HEDW.) SCHWAEGR.         BOG
C  3-B03 POLYTRICHUM JUNIPERINUM HEDW. VAR. GRACILIUS BOG
C  3-A05  SPHAGNUM FUSCUM (SCHIMP.) KLINGGR.            BOG
C  4+B06  CHAMAEDAPHNE CALYCULATA(L.)MOENCH             LAGG
C  4+A14  SALIX BEBBIANA SARG.                          LAGG
C  4+A12  CAREX ROSTRATA STOKES                         LAGG
C  4+A13  SALIX SERISSIMA (BAILEY) FERN.                LAGG
C  4+A11  CALAMAGROSTIS CANADENSIS (MICHX.) NUTT.       LAGG
C  4-B01  AULACOMNIUM PALUSTRE(HEDW.) SCHWAEGR.         LAGG
C  4-B02  HYPNUM PRATENSE KOCH EX SPRUCE                LAGG
C
      CHARACTER*1 $ZONE(24),$TYPE(24),$CLASS(24)
      CHARACTER*1 ZONE,TYPE,CLASS
      CHARACTER*1 $ZON(8),$TYP(8)
      CHARACTER*2 $SPEC(24)
      CHARACTER*2 SPEC
C
C  READING IN THE DATA CARD ORDER
C-------------------------------
C
      DATA $ZONE/'1','1','1','2','2','2','2','2','2',
     *           '3','3','3','3','3','3','3','3','4','4',
     *           '4','4','4','4','4'                      /
      DATA $TYPE/'+','+','-','+','+','+','+','+','-',
     *           '+','+','+','+','+','-','-','-','+','+',
```

```
     *           '+','+','+','-','-'                                /
      DATA $CLASS/'B','B','B','B','B','B','B','B','A',
     *            'B','B','B','B','B','B','B','A','B','A',
     *            'A','A','A','B','B'                               /
      DATA $SPEC/'15','08','04','15','08','06','10','07','05',
     *           '06','08','09','10','07','01','03','05','06','14',
     *           '12','13','11','01','02'                          /
      DATA $ZON/'1','1','2','2','3','3','4','4'/
      DATA $TYP/'+','-','+','-','+','-','+','-'/
      DATA $A/'ZTCS'/,$B/'LP1 '/,$C/'PLP2'/,$D/'FFP3'/,$E/'SP4'/,
     *$F/'RSP5'/,$G/'CORF'/,$H/'BIOM'/,$R/'PROD'/
      CHARACTER*5 $S/'PRODC'/
C
C  PRODUCING A TITLE CARD FOR THE PRINT OUT
C-----------------------------------------
C
    1 READ(IN,101,END=41000) TITLE
      WRITE(OUT,102) TITLE
  101 FORMAT(A80)
  102 FORMAT('1',A80//)
      OK=.TRUE.
C  ---
  199 FORMAT(' ')
C  --
C
C READING IN THE DATA ,CHECKING TO SEE THAT IT IS CODED CORRECTLY
C---------------------------------------------------------------
C
1000  DO 1001 I=1,24
      READ(IN,1101) ZONE,TYPE,CLASS,SPEC,(COMP(I,J),J=1,5),CORF(I),
     * BIOM(I),PROD(I),PRODC(I)
C COMP(I,J) = PRODUCTION VALUES WGT/UNIT AREA FOR FIVE AERIAL
C               PLANT COMPONENTS
C CORF(I) = CORRECTION FACTOR USED TO ACCOUNT FOR PRODUCTION
C           BY UNMEASURED SPECIES
C BIOM(I) = TOTAL BIOMASS (WGT/UNIT AREA) OF AERIAL PLANT COMPONENTS
C PROD(I) = TOTAL WGT/UNIT AREA OF AERIAL COMPONENTS ADDED TO PEAT
C PRODC(I) = TOTAL WGT/UNIT AREA OF AERIAL COMPONENTS ADDED TO PEAT,
C             MINUS DECOMPOSITION WEIGHT LOSS OVER ONE YEAR'S TIME
 1101 FORMAT(3A1,A2,5F7.2,F6.3,3F7.2)
      IF( (ZONE.EQ.$ZONE(I)) .AND. (TYPE.EQ.$TYPE(I)) .AND.
     * (CLASS.EQ.$CLASS(I)) .AND. (SPEC.EQ.$SPEC(I)) ) GO TO 1001
ON*   A CHARACTER VARIABLE IS USED WITH A RELATIONAL OPERATOR
ON*   A CHARACTER VARIABLE IS USED WITH A RELATIONAL OPERATOR
ON*   A CHARACTER VARIABLE IS USED WITH A RELATIONAL OPERATOR
ON*   A CHARACTER VARIABLE IS USED WITH A RELATIONAL OPERATOR
      WRITE(OUT,1102) I
      OK=.FALSE.
 1102 FORMAT('0**ERROR** COLS 1-5 OF INPUT CARD',I3,'DON''T CHECK')
 1001 CONTINUE
      IF(.NOT.OK) STOP
C
C WRITING OUT THE DATA INPUT FOR EACH SPECIES
C-------------------------------------------
C
      WRITE(OUT,199)
      WRITE(OUT,777) $A,$B,$C,$D,$E,$F,$G,$H,$R,$S
  777 FORMAT(' ',A4,4X,4(A4,3X),A4,1X,A4,4X,2(A4,3X),A5)
 1120 DO 1141 I=1,24
 1141 WRITE(OUT,1121) $ZONE(I),$TYPE(I),$CLASS(I),$SPEC(I),(COMP(I,J),
     *=1,5),CORF(I),BIOM(I),PROD(I),PRODC(I)
 1121 FORMAT(' ',3A1,A2,5F7.2,F6.3,3F7.2)
C
C
C THIS PART OF THE PROGRAMME CALCULATES THE ANNUAL PRODUCTION
```

```
C BY PEATLAND VEGETATION
C-------------------------
C
C2 CALCULATING THE TOTAL PRODUCTION OF FIVE AERIAL COMPONENTS,
C2 C SUB P1 - C SUB P5,FOR EACH SPECIES
C-------------------------------------
C
      WRITE(OUT,199)
2000  DO 3001 I=1,24
      SUM=0.
      DO 2002 J=1,5
 2002 SUM=SUM+COMP(I,J)
      C2(I)=SUM
 3001 WRITE(OUT,2101) $ZONE(I),$TYPE(I),$CLASS(I),$SPEC(I),SUM
 2101 FORMAT(' ','SUM OF C SUB P1 - C SUB P5 FOR SPECIES ',3A1,A2,' IS '
     *,F8.2)
C
C4 FINDING THE AERIAL PRODUCTION,SUM OF C SUB P1 - C SUB P5,
C4 FOR ALL IMPORTANT VASCULAR AND NON-VASCULAR SPECIES
C  ------------------------------------------------------
C
 4000 CALL COMPRS(C4,C2)
      WRITE(OUT,199)
 5000 DO 5001 I=1,8
 5001 WRITE(OUT,5101) $ZON(I),$TYP(I),C4(I)
 5101 FORMAT(' ','ZONE ',A1,' TYPE ',A1,' PRODUCTION IS ',F8.2)
C
C6 MULTIPLYING THE PRODUCTION CALCULATED FOR IMPORTANT SPECIES
C6 BY THE CORRECTION FACTOR FOR PRODUCTION BY UNMEASURED SPECIES
C-------------------------------------------------------------
C
6000  DO 7001 I=1,24
      C6(I)=C2(I)*CORF(I)
7001   CONTINUE
C
C8 CALCULATING THE CORRECTED AERIAL PRODUCTION FOR VASCULAR AND
C8 NON-VASCULAR SPECIES IN EACH OF THE FOUR ZONES
C-----------------------------------------------
C
 8000 CALL COMPRS(C8;C6)
      WRITE(OUT,199)
 9000 DO 9001 I=1,8
 9001 WRITE(OUT,9101) $ZON(I),$TYP(I),C8(I)
 9101 FORMAT(' ','ZONE ',A1,' TYPE ',A1,'PRODUCTION CORRECTED FOR UNMEAS
     *URED SPECIES IS ',F8.2)
C
C10 CALCULATING TOTAL AERIAL PRODUCTION IN THE FOUR ZONES
C--------------------------------------------------------
C
10000 DO 10001 I=1,4
10001 C10(I)=C8(2*I-1)+C8(2*I)
      WRITE(OUT,199)
11000 DO 11001 I=1,4
11001 WRITE(OUT,11101) I,C10(I)
11101 FORMAT(' ','AERIAL PRODUCTION FOR ZONE ',I1,' IS ',F8.2)
C
C13 ADDING SUBSURFACE PRODUCTION TO AERIAL TOTALS CALCULATED EARLIER
C13 FOR EACH OF THE FOUR ZONES
C-----------------------------
C
12000 READ(IN,12101) SUBPRD,SUBTBL
C SUBPRD(I) = ZONAL SUBSURFACE PRODUCTION (WGT/UNIT AREA)
C SUBTBL(I) = ZONAL SUBSURFACE BIOMASS (WGT/UNIT AREA)
12101 FORMAT(8F8.2)
C
```

```
C WRITING OUT THE DATA VALUES FOR 'SUBPRD' AND 'SUBTBL'
C-------------------------------------------------------------
C
      WRITE(OUT,199)
12302 WRITE(OUT,12402) SUBPRD
12402 FORMAT(' ','SUBSURFACE PRODUCTION (ZONES 1-4) IS ',4F8.2)
      WRITE(OUT,12403) SUBTBL
12403 FORMAT(' ','SUBSURFACE BIOMASS (ZONES 1-4) IS ',4F8.2)
C
      WRITE(OUT,199)
13000 DO 14001 I=1,4
      C13(I)=C10(I)+SUBPRD(I)
14001 WRITE(OUT,13101) I,C13(I)
13101 FORMAT(' ','AERIAL AND SUBSURFACE PRODUCTION,C SUB P1 - C SUB P8,
     *IN ZONE ',I1,' IS ',F8.2)
C
C15 CORRECTION FOR LOSSES THROUGH HERBIVORE CONSUMPTION,C SUB CP,
C15 AND PLANT SECRETIONS,S SUB CP,B
C15 PRODUCTION INCREASED BY 6% IN EACH ZONE
C-----------------------------------------------
C
      WRITE(OUT,199)
15000 DO 15001 I=1,4
      C15(I)=C13(I)*1.06
15001 WRITE(OUT,15101) I,C15(I)
15101 FORMAT(' ','TOTAL PRODUCTION FOR ZONE ',I1,' IS ',F8.2)
C
C
C
C THIS PART OF THE PROGRAMME CALCULATES BIOMASS VALUES
C-------------------------------------------------------------
C
C18 CALCULATING THE TOTAL BIOMASS VALUE FOR AERIAL COMPONENTS,
C18 FOR BOTH VASCULAR AND NON-VASCULAR SPECIES IN ALL ZONES
C   ---------------------------------------------------------
C
18000 CALL COMPRS(C18,BIOM)
      WRITE(OUT,199)
18001 DO 18200 I=1,8
18200 WRITE(OUT,18201) $ZON(I),$TYP(I),C18(I)
18201 FORMAT(' ','ZONE ',A1,' TYPE ',A1,' BIOMASS IS ',F8.2)
C
C19 CALCULATION OF THE BIOMASS CORRECTION FACTOR FOR UNMEASURED SPECIES
C19 USING THE UNCORRECTED AND CORRECTED ZONAL PRODUCTION DATA CALCULATED
C19 EARLIER,IE. C8 DIVIDED BY C4
C-----------------------------------
C
      WRITE(OUT,199)
19000 DO 20001 I=1,8
      C19(I)=C8(I)/C4(I)
20001 WRITE(OUT,19101) $ZON(I),$TYP(I),C19(I)
19101 FORMAT(' ','ZONE ',A1,' TYPE ',A1,' CORRECTION FACTOR FOR OTHER SP
     *ECIES IS ',F8.2)
C
C21 CORRECTING AERIAL BIOMASS VALUES FOR OTHER SPECIES
C-------------------------------------------------------------
C
      WRITE(OUT,199)
21000 DO 22001 I=1,8
      C21(I)=C19(I)*C18(I)
22001 WRITE(OUT,21101) $ZON(I),$TYP(I),C21(I)
21101 FORMAT(' ','ZONE ',A1,' TYPE ',A1,' BIOMASS CORRECTED FOR UNMEASUR
     *ED SPECIES IS ',F8.2)
C
C23 FORMING AERIAL BIOMASS TOTALS FOR EACH OF THE FOUR ZONES
```

```
C ------------------------------------------------------------------
C
23000 DO 23001 I=1,4
23001 C23(I)=C21(2*I-1)+C21(2*I)
C
C24 ADDING SUBSURFACE BIOMASS VALUES
C-----------------------------------
C
      WRITE(OUT,199)
24000 DO 24001 I=1,4
      C24(I) = (C23(I) + SUBTBL(I))
24001 WRITE(OUT,24101) I,C24(I)
24101 FORMAT(' ','TOTAL BIOMASS FOR ZONE ',I1,' IS ',F8.2)
C
C25 CALCULATING THE P/B RATIO,TOTAL NET PRIMARY PRODUCTION
C25 DIVIDED BY TOTAL BIOMASS
C-----------------------------
      DO 25000 I = 1,4
25000 C25(I) = C15(I)/C24(I)
      WRITE(OUT,199)
      DO 25001 I = 1,4
25001 WRITE(OUT,25002) I,C25(I)
25002 FORMAT(' ',' P/B RATIO IN ZONE ',I1,' IS ',F8.2)
C
C
C
C THIS PART OF THE PROGRAMME DETERMINES THE ANNUAL ACCUMULATION OF PEAT
C-----------------------------------------------------------------------
C
C27 CALCULATING THE AMOUNT OF CURRENT AERIAL PRODUCTION ADDED TO PEAT B
C27 VASCULAR AND NON-VASCULAR SPECIES IN EACH OF THE FOUR ZONES
C-----------------------------------------------------------------------
C
27000 CALL COMPRS(C27,PROD)
C
C29 CORRECTING THE AMOUNT ADDED BY VASCULAR SPECIES FOR OTHER UNMEASURE
C29 SPECIES AND ALSO FOR WOODY LITTER (23%)
C-----------------------------------------
C
29000 DO 29001 I=1,4
29001 C29(I)=C19(2*I-1)*C27(2*I-1)*1.23
C
C30 TOTAL AERIAL INPUT BY BOTH VASCULAR AND NON-VASCULAR SPECIES
C--------------------------------------------------------------
C
30000 DO 30001 I=1,4
30001 C30(I)=C29(I)+C27(2*I)*C19(2*I)
      WRITE(OUT,199)
31000 DO 31001 I=1,4
31001 WRITE(OUT,31101) I,C30(I)
31101 FORMAT(' ','ZONE ',I1,' AERIAL COMPONENT ACCUMULATION IS ',F8.2)
C
C33 ADDING SUBSURFACE PRODUCTION VALUES AND LEACHATE VALUES(S SUB CP,B)
C33 TO THE ACCUMULATION TOTALS FOR EACH OF THE FOUR ZONES
C-------------------------------------------------------
C
      WRITE(OUT,199)
33000 DO 34001 I=1,4
      C33(I)=C30(I)+SUBPRD(I)+(.01*C15(I))
34001 WRITE(OUT,33101) I,C33(I)
33101 FORMAT(' ','TOTAL INITIAL WEIGHT OF PEAT ACCUMULATED ANNUALLY,A S
     *B I, IN ZONE ',I1,' IS ',F8.2)
C
C3627 CALCULATING THE AMOUNT OF THIS PEAT REMAINING AFTER
C3627 ONE YEAR (A' SUB I)
```

```
C-------------------------
C
      CALL COMPRS(C3627,PRODC)
      DO 36291 I=1,4
36291 C3629(I)=C19(2*I-1)*C3627(2*I-1)*1.23
      DO 36301 I=1,4
36301 C3630(I)=C3629(I)+C3627(2*I)*C19(2*I)
C
      READ(IN,36202) SUBDEC
C SUBDEC(I) = TOTAL ZONAL WGT/UNIT AREA OF SUBSURFACE COMPONENTS ADDED
C             TO PEAT,MINUS DECOMPOSITION WEIGHT LOSS OVER ONE YEAR'S TIME
36202 FORMAT(4F8.2)
C
C WRITING OUT THE DATA VALUES FOR 'SUBDEC'
C-----------------------------------------
C
      WRITE(OUT,199)
36511 WRITE(OUT,36551) SUBDEC
36551 FORMAT(' ','VALUES FOR SUBDEC IN ZONES 1-4 ARE ',4F8.2)
C
      DO 36331 I=1,4
36331 C3633(I)= C3630(I)+SUBDEC(I) -(.01*C15(I))
      WRITE(OUT,199)
37000 DO 37001 I=1,4
37001 WRITE(OUT,37101) I,C3633(I)
37101 FORMAT(' ','TOTAL WEIGHT OF ACCUMULATED PEAT REMAINING AFTER ONE Y
     *EAR,A'' SUB I,IN ZONE ',I1,' IS ',F8.2)
C
C39 CALCULATING SURFACE ACCUMULATION RATIO,
C39 I.E. AMOUNT REMAINING AFTER ONE YEAR DIVIDED BY THE ORIGINAL
C39 NET PRIMARY PRODUCTION TOTAL
C-------------------------------
38101 DO 38102 I = 1,4
38102 C39(I) = C3633(I)/C15(I)
      WRITE(OUT,199)
38103 DO 38104 I = 1,4
38104 WRITE(OUT,38105) I,C39(I)
38105 FORMAT(' ',' ANNUAL SURFACE ACCUMULATION RATIO IN ZONE ',I1,' IS '
     *,F8.2)
C
      GO TO 1
41000 STOP
      END
C

      SUBROUTINE COMPRS(C4,C2)
      REAL*4 C4(8),C2(24)
 4000 C4(1)=C2(1)+C2(2)
      C4(2)=C2(3)
      C4(3)=C2(4)+C2(5)+C2(6)+C2(7)+C2(8)
      C4(4)=C2(9)
      C4(5)=C2(10)+C2(11)+C2(12)+C2(13)+C2(14)
      C4(6)=C2(15)+C2(16)+C2(17)
      C4(7)=C2(18)+C2(19)+C2(20)+C2(21)+C2(22)
      C4(8)=C2(23)+C2(24)
      RETURN
      END
```

| ZTCS | LP1 | PLP2 | FFP3 | SP4 | RSP5 | CORF | BIOM | PROD | PRODC |
|---|---|---|---|---|---|---|---|---|---|
| 1+B15 | 118.40 | 130.50 | 0.30 | 27.10 | 26.20 | 1.000 | 4186.00 | 118.70 | 86.30 |
| 1+B08 | 24.30 | 0.00 | 1.90 | 3.80 | 22.80 | 1.213 | 134.56 | 22.40 | 15.00 |
| 1-B04 | 107.70 | 0.00 | 0.00 | 0.00 | 0.00 | 1.080 | 185.20 | 107.70 | 81.10 |
| 2+B15 | 34.90 | 15.50 | 0.20 | 9.20 | -1.40 | 1.230 | 367.80 | 35.10 | 23.20 |
| 2+B08 | 76.20 | 0.00 | 0.30 | 10.10 | 36.40 | 1.053 | 237.00 | 65.50 | 53.80 |
| 2+B06 | 24.10 | 0.00 | 12.20 | 10.90 | 10.20 | 1.053 | 140.50 | 20.50 | 14.70 |
| 2+B10 | 29.10 | 0.00 | 10.80 | 10.00 | -2.50 | 1.053 | 56.30 | 39.90 | 26.20 |
| 2+B07 | 7.70 | 0.00 | 3.30 | 1.50 | 0.90 | 1.053 | 27.60 | 8.00 | 6.90 |
| 2-A05 | 7.10 | 0.00 | 0.00 | 0.00 | 0.00 | 2.390 | 39.20 | 7.10 | 7.00 |
| 3+B06 | 42.40 | 0.00 | 24.40 | 15.50 | 23.80 | 1.027 | 151.00 | 37.80 | 26.40 |
| 3+B08 | 46.80 | 0.00 | 1.40 | 8.20 | 11.70 | 1.027 | 128.40 | 41.30 | 35.60 |
| 3+B09 | 15.10 | 0.00 | 18.30 | 4.90 | 12.10 | 1.027 | 35.50 | 33.40 | 31.00 |
| 3+B10 | 27.80 | 0.00 | 13.80 | 8.50 | 2.60 | 1.027 | 53.40 | 41.60 | 25.50 |
| 3+B07 | 14.60 | 0.00 | 7.80 | 3.60 | 4.90 | 1.027 | 44.30 | 16.30 | 10.50 |
| 3-B01 | 5.40 | 0.00 | 0.00 | 0.00 | 0.00 | 1.150 | 20.10 | 5.40 | 5.00 |
| 3-B03 | 35.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.150 | 42.30 | 35.00 | 30.10 |
| 3-A05 | 7.80 | 0.00 | 0.00 | 0.00 | 0.00 | 1.150 | 51.80 | 7.80 | 7.80 |
| 4+B06 | 70.30 | 0.00 | 26.20 | 27.90 | 102.90 | 1.156 | 452.10 | 54.60 | 45.00 |
| 4+A14 | 117.60 | 0.00 | 18.20 | 21.60 | 61.70 | 2.160 | 998.20 | 97.40 | 69.10 |
| 4+A12 | 81.90 | 0.00 | 0.10 | 34.00 | 0.00 | 1.156 | 43.50 | 97.10 | 75.70 |
| 4+A13 | 3.70 | 0.00 | 0.60 | 6.00 | 1.00 | 2.160 | 66.90 | 3.10 | 2.30 |
| 4+A11 | 21.70 | 0.00 | 0.10 | 26.50 | 0.00 | 1.156 | 23.20 | 27.30 | 21.00 |
| 4-B01 | 35.90 | 0.00 | 0.00 | 0.00 | 0.00 | 1.130 | 38.80 | 35.90 | 33.20 |
| 4-B02 | 31.20 | 0.00 | 0.00 | 0.00 | 0.00 | 1.130 | 38.60 | 31.20 | 24.00 |

| | |
|---|---|
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 1+B15 IS | 302.50 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 1+B08 IS | 52.80 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 1-B04 IS | 107.70 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 2+B15 IS | 58.40 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 2+B08 IS | 123.00 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 2+B06 IS | 57.40 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 2+B10 IS | 47.40 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 2+B07 IS | 13.40 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 2-A05 IS | 7.10 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 3+B06 IS | 106.10 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 3+B08 IS | 68.10 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 3+B09 IS | 50.40 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 3+B10 IS | 52.70 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 3+B07 IS | 30.90 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 3-B01 IS | 5.40 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 3-B03 IS | 35.00 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 3-A05 IS | 7.80 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 4+B06 IS | 227.30 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 4+A14 IS | 219.10 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 4+A12 IS | 116.00 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 4+A13 IS | 11.30 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 4+A11 IS | 48.30 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 4-B01 IS | 35.90 |
| SUM OF C SUB P1 - C SUB P5 FOR SPECIES 4-B02 IS | 31.20 |

| | |
|---|---|
| ZONE 1 TYPE + PRODUCTION IS | 355.30 |
| ZONE 1 TYPE - PRODUCTION IS | 107.70 |
| ZONE 2 TYPE + PRODUCTION IS | 299.60 |
| ZONE 2 TYPE - PRODUCTION IS | 7.10 |
| ZONE 3 TYPE + PRODUCTION IS | 308.20 |
| ZONE 3 TYPE - PRODUCTION IS | 48.20 |
| ZONE 4 TYPE + PRODUCTION IS | 622.00 |
| ZONE 4 TYPE - PRODUCTION IS | 67.10 |

ZONE 1 TYPE +PRODUCTION CORRECTED FOR UNMEASURED SPECIES IS 366.5

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ZONE 1 TYPE -PRODUCTION CORRECTED FOR UNMEASURED SPECIES IS    116.32
ZONE 2 TYPE +PRODUCTION CORRECTED FOR UNMEASURED SPECIES IS    325.82
ZONE 2 TYPE -PRODUCTION CORRECTED FOR UNMEASURED SPECIES IS     16.97
ZONE 3 TYPE +PRODUCTION CORRECTED FOR UNMEASURED SPECIES IS    316.52
ZONE 3 TYPE -PRODUCTION CORRECTED FOR UNMEASURED SPECIES IS     55.43
ZONE 4 TYPE +PRODUCTION CORRECTED FOR UNMEASURED SPECIES IS    950.35
ZONE 4 TYPE -PRODUCTION CORRECTED FOR UNMEASURED SPECIES IS     75.82

AERIAL PRODUCTION FOR ZONE 1 IS    482.86
AERIAL PRODUCTION FOR ZONE 2 IS    342.78
AERIAL PRODUCTION FOR ZONE 3 IS    371.95
AERIAL PRODUCTION FOR ZONE 4 IS   1026.18

SUBSURFACE PRODUCTION (ZONES 1-4) IS   186.90  593.50 1461.10  512.50
SUBSURFACE BIOMASS (ZONES 1-4) IS  2280.00 1644.00 1956.00 1304.00

AERIAL AND SUBSURFACE PRODUCTION,C SUB P1 - C SUB P8, IN ZONE 1 IS    669.76
AERIAL AND SUBSURFACE PRODUCTION,C SUB P1 - C SUB P8, IN ZONE 2 IS    936.28
AERIAL AND SUBSURFACE PRODUCTION,C SUB P1 - C SUB P8, IN ZONE 3 IS   1833.05
AERIAL AND SUBSURFACE PRODUCTION,C SUB P1 - C SUB P8, IN ZONE 4 IS   1538.68

TOTAL PRODUCTION FOR ZONE 1 IS    709.95
TOTAL PRODUCTION FOR ZONE 2 IS    992.46
TOTAL PRODUCTION FOR ZONE 3 IS   1943.03
TOTAL PRODUCTION FOR ZONE 4 IS   1631.00

ZONE 1 TYPE + BIOMASS IS   4320.56
ZONE 1 TYPE - BIOMASS IS    185.20
ZONE 2 TYPE + BIOMASS IS    829.20
ZONE 2 TYPE - BIOMASS IS     39.20
ZONE 3 TYPE + BIOMASS IS    412.60
ZONE 3 TYPE - BIOMASS IS    114.20
ZONE 4 TYPE + BIOMASS IS   1583.90
ZONE 4 TYPE - BIOMASS IS     77.40

ZONE 1 TYPE + CORRECTION FACTOR FOR OTHER SPECIES IS      1.03
ZONE 1 TYPE - CORRECTION FACTOR FOR OTHER SPECIES IS      1.08
ZONE 2 TYPE + CORRECTION FACTOR FOR OTHER SPECIES IS      1.09
ZONE 2 TYPE - CORRECTION FACTOR FOR OTHER SPECIES IS      2.39
ZONE 3 TYPE + CORRECTION FACTOR FOR OTHER SPECIES IS      1.03
ZONE 3 TYPE - CORRECTION FACTOR FOR OTHER SPECIES IS      1.15
ZONE 4 TYPE + CORRECTION FACTOR FOR OTHER SPECIES IS      1.53
ZONE 4 TYPE - CORRECTION FACTOR FOR OTHER SPECIES IS      1.13

ZONE 1 TYPE + BIOMASS CORRECTED FOR UNMEASURED SPECIES IS  4457.32
ZONE 1 TYPE - BIOMASS CORRECTED FOR UNMEASURED SPECIES IS   200.02
ZONE 2 TYPE + BIOMASS CORRECTED FOR UNMEASURED SPECIES IS   901.76
ZONE 2 TYPE - BIOMASS CORRECTED FOR UNMEASURED SPECIES IS    93.69
ZONE 3 TYPE + BIOMASS CORRECTED FOR UNMEASURED SPECIES IS   423.74
ZONE 3 TYPE - BIOMASS CORRECTED FOR UNMEASURED SPECIES IS   131.33
ZONE 4 TYPE + BIOMASS CORRECTED FOR UNMEASURED SPECIES IS  2420.04
ZONE 4 TYPE - BIOMASS CORRECTED FOR UNMEASURED SPECIES IS    87.46

TOTAL BIOMASS FOR ZONE 1 IS  6937.33
TOTAL BIOMASS FOR ZONE 2 IS  2639.44
TOTAL BIOMASS FOR ZONE 3 IS  2511.07
TOTAL BIOMASS FOR ZONE 4 IS  3811.50

 P/B RATIO IN ZONE 1 IS     0.10
 P/B RATIO IN ZONE 2 IS     0.38
 P/B RATIO IN ZONE 3 IS     0.77
 P/B RATIO IN ZONE 4 IS     0.43

ZONE 1 AERIAL COMPONENT ACCUMULATION IS    295.36
ZONE 2 AERIAL COMPONENT ACCUMULATION IS    243.03
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ZONE 3 AERIAL COMPONENT ACCUMULATION IS    270.68
ZONE 4 AERIAL COMPONENT ACCUMULATION IS    601.09

TOTAL INITIAL WEIGHT OF PEAT ACCUMULATED ANNUALLY,A SUB I, IN ZONE 1 IS    489.36
TOTAL INITIAL WEIGHT OF PEAT ACCUMULATED ANNUALLY,A SUB I, IN ZONE 2 IS    846.45
TOTAL INITIAL WEIGHT OF PEAT ACCUMULATED ANNUALLY,A SUB I, IN ZONE 3 IS   1751.21
TOTAL INITIAL WEIGHT OF PEAT ACCUMULATED ANNUALLY,A SUB I, IN ZONE 4 IS   1129.90

VALUES FOR SUBDEC IN ZONES 1-4 ARE   135.10  464.10 1234.60  394.10

TOTAL WEIGHT OF ACCUMULATED PEAT REMAINING AFTER ONE YEAR,A' SUB I,IN ZONE 1 IS    344.13
TOTAL WEIGHT OF ACCUMULATED PEAT REMAINING AFTER ONE YEAR,A' SUB I,IN ZONE 2 IS    637.84
TOTAL WEIGHT OF ACCUMULATED PEAT REMAINING AFTER ONE YEAR,A' SUB I,IN ZONE 3 IS   1427.46
TOTAL WEIGHT OF ACCUMULATED PEAT REMAINING AFTER ONE YEAR,A' SUB I,IN ZONE 4 IS    842.91

 ANNUAL SURFACE ACCUMULATION RATIO IN ZONE 1 IS      0.48
 ANNUAL SURFACE ACCUMULATION RATIO IN ZONE 2 IS      0.64
 ANNUAL SURFACE ACCUMULATION RATIO IN ZONE 3 IS      0.73
 ANNUAL SURFACE ACCUMULATION RATIO IN ZONE 4 IS      0.52
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C. Glossary

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| Accumulation: | income of dry matter resulting from net primary production minus the amount lost through decomposition. |
| Biomass: | the weight of all living material present in a unit area at a given time. |
| Bog: | a peat-covered or peat-filled area with vegetation characterized by ericaceous shrubs and mosses, mostly Sphagnum spp. (Heinselman, 1963, p. 373; Carpenter, 1956, p. 46; Dansereau and Segadas-Vianna, 1952, p. 490). |
| Decomposition: | the separation or resolution (as of a substance) into constituent parts or elements or into simpler compounds. (Webster's Third New International Dictionary, 1967, p. 587) |
| Fen: | European term applied to grass, sedge, or reed-covered peatlands, often with some shrub cover and sometimes a scanty tree layer. Water table at surface most of time. Waters and peats not very acid. (Heinselman, 1963, p. 373) |
| Lagg: | a marginal fen. (Sjors, 1948, p. 286) |
| Muskeg: | a large expanse of Sphagnum peatland bearing stunted black spruce and tamarack. (Heinselman, 1963, p. 374) See also Ritchie (1956, p. 547) |
| Peat: | peat itself is simply an accumulation of plant remains in varying stages of alteration by chemical, physical and microbial processes. (Heinselman, 1963, p. 329) |
| Peatland: | all classes of peat-covered land. (Heinselman, 1963, p. 374) |

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| Primary production: | the weight of new organic material created by photosynthesis, or the energy which this represents. It is the increase observed in the biomass of green plants over a period of time plus any losses (e.g., excretion, respiration, damage, death, or growing). Gross production is the observed change in biomass plus all losses, while net production excludes the loss through respiration (Westlake, 1966, p. 316). |
| Semideciduous: | refers to plants which retain their leaves until the next season's leaves have developed, as opposed to plants on which the leaves persist for many years. Overlaps with the term "evergreen". (Lems, 1956, p. 199) |