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NET PRIMARY PRODUCTIVITY AND BIOMASS OF A MATURE SOUTHERN MICHIGAN BOG

By

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INTRODUCTION

Primary productivity is the rate at which photosynthesis binds energy or creates organic matter per unit area per unit time. Net primary production is the amount of primary production remaining after the respiratory uses of the green plant producers have been subtracted. All heterotrophic organisms depend upon the primary production as the ultimate source of their food-derived energy and for much of their structural material. In addition, in many situations, the biomass produced is also important in controlling the physical and chemical environment of living organisms. Bogs represent a good example of such a situation. In bog ecosystems, accumulation of organic matter in the form of peat exerts a profound influence on both the biotic and the abiotic components of the system. Productivity estimates, combined with estimates of decomposition rates, should prove useful in understanding the dynamics of bog systems.

There is no general agreement on the exact definition of the term "bog". Dansereau and Segadas-Vianna (1952) pointed this out and outlined a number of bog definitions that had been proposed by other researchers. The definition I prefer is one of the simplest and narrowest of these but seems to aptly specify those areas I would intuitively consider to be bogs. This is the definition favored by Oswald (1933) that applies the term bog only to those peat accumulating areas dominated by an ericaceous vegetation underlain by an essentially continuous blanket of *Sphagnum* spp. mosses.

Most research conducted on bogs has been concerned with describing the vegetation, flora, peat chemistry, successional history, or pollen records. Few researchers have examined the characteristic which was the focus of this study. Examples of such studies on net primary productivity in bog systems are those of Forrest (1971), Forrest and Smith (1974), and Reader and Stewart (1972). However, all three of these studies dealt with areas which were markedly different both physically and geographically from the bog that was the subject of this study. No further bog productivity studies were revealed in a literature search using Biological Abstracts and recent editions of botanical and ecological journals found in the Michigan State University library.

Field observations, measurements, and sampling for the research project were conducted during April through November of 1978. Crum (1976) was used as the nomenclatural authority for moss species while Gleason and Cronquist (1963) was used for vascular plants.

STUDY AREA

This study was conducted in a section of the Waterloo Recreation Area designated as a natural area and commonly known as the Waterloo Black Spruce Bog. The bog is located in the SW¼ of the NE¼ of Section 16 of Waterloo Township in northeastern Jackson County, Michigan.

An aerial view of the Waterloo Bog is found in Figure 1. Figure 2 presents a ground level view of the vegetation.

Waterloo Bog lies in a formerly glaciated region covered by glacial outwash which includes several small kettle lakes. The bog itself occupies a kettle depression that has been filled by peat and inorganic sediments. Peat and inorganic cores removed from the bog revealed that total depth from the Sphagnum surface to the bottom of the sediments ranged to over 11 m in certain locations. This depth represents the limit of the coring device used. Peat depth varies from about 1 m to about 7 m. Less fibrous largely organic sediments ranged down to 9 m in depth, as measured from the Sphagnum surface, with thickness varying from 0 m to about 2 m. This layer was always overlain by at least a shallow layer of peat. A layer of gray calcium carbonate-rich sediment was found beneath much of the organic material. Thickness of this stratum reached a maximum value of over 3 m. Remnants of gastropod shells were found in much of this sediment.

Figure 1. Aerial photograph of Waterloo Bog

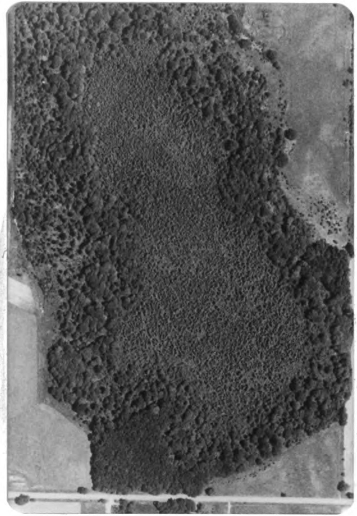


Figure 2. Ground level photograph of Waterloo Bog

Approximately 15 hectares are presently covered by bog vegetation in the study area. The basin is approximately two times as long as broad with its long axis oriented just west of north.

Spagnum magellanicum Brid, Sphagnum recurvum P. Beauv., and Sphagnum subnitens Russ and Warnst provide the dominant ground cover. Scattered patches of other moss species are found relatively infrequently. Herbaceous species found growing on the moss carpet include pitcher plant (Sarracenia purpurea L.), sundew (Drosera rotundifolia L.), cranberry (Vaccinium macrocarpon Ait.), stemless lady-slipper (Cypripedium acaule Ait.), Canada mayflower Maianthemum canadense Desf.), starflower (Trientalis borealis Raf.), Indian pipe (Montropa uniflora L.), goldthread (Coptis trifolia Salisb.), and several species of sedges and rushes. None of these herbaceous species forms an extensive cover in any location within the Waterloo Bog.

Three species of woody plants provide a nearly complete cover over the bog area. Two of these species are trees (Larix laricina K. Koch and Picea mariana BSP.) while the third is a shrub (Vaccinium corymbosum L.). Scattered individuals or clumps of red maple (Acer rubrum L.), poison sumac (Toxicodendron vernix L.), Michigan holly (Ilex verticillata Gray), and green alder (Nemopanthus mucronatus Trel.) occur throughout the bog but do not cover any sizeable expanses.

Thompson, et al. (1966; date unknown) described the physical site, vegetation, and flora of the Waterloo Bog area in two short papers. Both of these papers were internal reports of the Michigan Natural Areas council. This organization was instrumental in the preservation of the Waterloo Bog.

The bog is bordered on the east, south, and west by a narrow woodland border. To the north there is a much more extensive woodlot. The wooded area slopes upward from the bog on the east, south, and west while to the north there is an essentially flat area that eventually slopes away from the bog. Elevation of the bog surface is about 287 m above sea level. Drainage ditches run parallel to the outer edges of the woodland border. These ditches serve to drain the farmland adjacent to the woodland. Water is conducted from the fields east and west of the bog in a northwesterly direction before it enters Orchard Creek, a tributary of the Grand River which eventually flows into Lake Michigan.

Red maple is the dominant species of the woodland border. Common woody associates include quaking aspen (Populus tremuloides Michx.), black cherry (Prunus serotina Ehrh.), red oak (Quercus rubra L.), white ash (Fraxinus americana L.), witch hazel (Hamamelis virginiana L.), and meadowsweet (Spirea alba DuRoi). Other woody species become more abundant in the wetter portions of the forest ring located immediately adjacent to the bog. These include chokeberry (Aronia melanocarpa Ell.), Michigan holly, green alder, and highbush blueberry (Vaccinium corymbosum).

Veatch et al. (1930) describe the climate of Jackson County as being characterized by fairly cold winters, mild summers, and moderate precipitation. Prevailing winds are westerly and seldom of high velocity. Humidity is relatively high. Sunshine is 35 to 40 percent of that possible. A climatological summary for the city of Jackson for the years 1940 through 1969 was obtained from the Michigan Department of Agriculture Weather Service. Jackson is located about 20 miles southwest of the Waterloo Bog. The average yearly temperature and precipitation were 8.9°C and 77 cm respectively. Precipitation was fairly evenly distributed throughout the year and included an average of 91 cm of snow. There was an average of 150 consecutive days per year during which the temperature did not drop below 0°C. This period typically extended from about May 10 to October 6. Overall, 1978 was slightly cooler (average temperature 8.3°C) and had slightly less precipitation (total precipitation 69.1 cm) than the averages given above. There was a span of 159 days from May 3 to October 9 where the temperature did not drop below 0°C. However, this period may have been shorter in the Waterloo Bog since bogs tend to be somewhat cooler than surrounding areas. The maximum temperature during 1978 of 38°C was reached on September 9. On February 2 the minimum temperature of -25°C was reached.

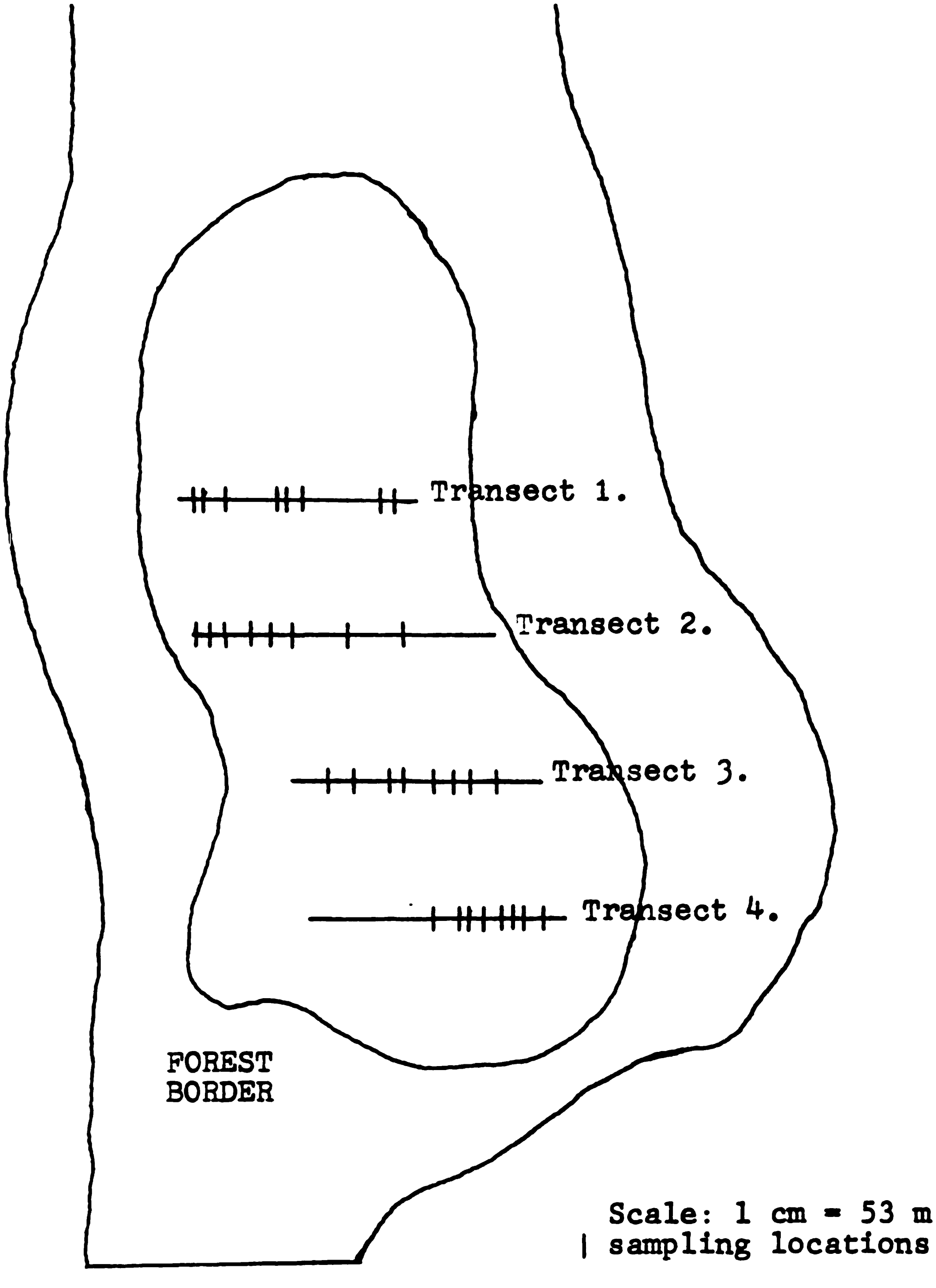
METHODS

At the beginning of the study period, four transect lines were run in an east to west direction for subsequent use in location of sites for vegetation analysis and sampling. The first of these was started about 100 m north of the southern end of the bog. Each of the three subsequent lines was parallel to the first line with spacing between the lines of approximately 100 m. Transect lines ranged in length from 165 m to 235 m. Their positions are indicated on the outline sketch of the bog in Figure 2.

Methods used for estimation of aboveground net primary productivity and biomass in the Waterloo Bog are outlined below. All losses due to herbivory and litterfall were assumed to be small and no attempt was made to estimate these parameters in this study. It was not possible to estimate belowground biomass and productivity since the study area is a protected natural area where the necessary excavation was not possible.

Figure 3

Transect placement in Waterloo Bog



Trees

Tree biomass and productivity were determined using the technique of dimension analysis or allometery as discussed by Whittaker and Marks (1975). This method is commonly used in dealing with uneven-sized stands of trees. It involves the development of regressions relating various fractions of production to the diameter at breast height (DBH) or to another easily measured dimension of the trees. Since the Waterloo Bog is a protected area, special adaptations as developed by Reiners (1972) were employed so that no trees needed to be destroyed.

The first step necessary in the estimation of biomass or productivity is the determination of tree densities in the area under consideration. In this study, counts and measurements of DBH were made in eight randomly selected 25 m^2 quadrats along each of the four transect lines. Positions of these quadrats are indicated on Figure 2. Trees of each species were tallied separately. Only individuals taller than 137 cm were treated as trees. DBH size distribution tables were then constructed for each of the two major tree species (*Picea* and *Larix*). These tables were used as the basis for selection of trees for extensive dimension analysis and sampling. Size distribution of the sample trees represented the size distribution of the tree populations.

Ten *Picea* and five *Larix* trees were subjected to the extensive dimension analysis procedure. This included a tally of all branches on each of the subject trees. Basal diameter (BD), length, condition (living or dead), and approximate position on the bole (bottom 0.2 of length to top 0.2 of length) was recorded for each branch. Branch BD distribution tables were next constructed for each of the analyzed trees. Separate tables were constructed for living and for dead branches. The living branch BD tables were used to select branches for harvest and weighing.

Five living branch BD sizes were selected for sampling from the BD distribution of each analyzed tree. Sample branch size distribution approximated the size class distribution of branches on subject trees. Branch harvest was conducted during late August to early September to coincide with peak biomass. To minimize impact of sampling on the health of the trees, only one branch was removed from each of the analyzed specimens. The other four branches were removed from four other trees of the same DBH size class as the trees that underwent dimension analysis. Each sample branch was aged using growth rings or bud scale scars. Branches were oven-dried to constant weight at 80°C. Weights of branch components -- current shoots, "other" wood and bark, dead wood, old leaves, and new leaves -- were determined using a Mettler electronic top-loading balance accurate to within a hundredth of a gram.

Diameter at ground height as well as DBH was measured for each of the trees subjected to dimension analysis. A core of wood and bark was removed from each of these trees at breast height. Bark thickness as well as thickness of each year's wood increment for each tree was determined in the lab to the nearest hundredth of a mm. In addition to the above cores, 32 cores of *Picea mariana* and *Larix laricina* were removed from selected trees of greater than eight cm DBH. This was done to gain a better idea of relative rates of tree growth through the bog. Trees for this purpose were those located the shortest distance, in each of four 90 degree quadrats, from each of ten evenly spaced points along the four transect lines. These cores underwent ring analysis in the same manner as the cores from the other trees. No cores were removed from trees in those quadrants in which no trees were present within 10 m of the corner of the quadrant. Ten *Picea* and ten *Larix* cores were subjected to wood and bark density determinations.

Biomass and productivity calculations began with a determination of these parameters for the branches on each of the fifteen trees chosen for dimension analysis. This was done through regression analysis utilizing dry biomass data collected on the sample branches. The logarithm of the branch BD was regressed against the log of each of the biomass components to develop branch biomass prediction equations for *Picea* and *Larix*. The BD value of each tallied branch was run through the equations and biomass totals for all components for all branches were summed separately for each sample tree. Logarithmic transformations of all data were necessary to normalize the data and make them more compatible with the underlying assumptions of regression analysis. However, conversion of the production estimates from the logarithmic back to the arithmetic form produces a systematic underestimate (Baskerville, 1973; Beauchamp and Olson, 1973). This results from the fact that if a distribution is normal in logarithms, the conversion of the predicted Y value from the logarithmic to the arithmetic form yields the arithmetic median rather than the desired mean at a given X value (Finney, 1941). The calculation of a correction factor for this bias was incorporated into the calculator programs used for estimating the biomass and productivity values. This correction factor was calculated using the method suggested by Baskerville (1973). Once estimates of the branch component weights for each of the analyzed trees were obtained, it was possible to develop regressions to predict the collective branch biomass of an entire tree from the tree's DBH value. This again involved logarithmic transformations of both the independent and dependent data sets. Prediction equations relating the log of the DBH to the logarithms of the masses of the leaf, current shoot, "other" wood and bark, and dead wood on living branch components were constructed. Bole wood and bark biomass prediction equations were developed using a bole volume estimate based on the relationship of volume being approximately equal to one-half basal area times height. Volume estimates were combined with wood and bark density estimates to yield biomass estimates. Tree branch and bole biomass prediction equations were used in conjunction with the tree DBH values from the 32 - 25 m^2 quadrats to estimate the aboveground biomass of the bog trees. Biomass values for trees other than Picea and Larix were estimated using the Larix prediction equations. All results were expressed as g/m^2.

Tree net primary productivity equations were developed in a fashion analagous to the biomass equations. That is, biomass values for sample branches were used to develop prediction equations for branch productivity on analyzed trees while these estimates for analyzed trees were used to develop prediction equations for whole tree productivities. Current shoot productivity was considered to be equal to the current shoot biomass. Leaf productivity estimation made use of biomass equations for the current season's leaves. Branch "other" wood and bark productivity prediction equations were constructed using biomass data from sample branches combined with age information on these branches. Log of branch age was first regressed against the log of "other" branch wood and bark biomass. Since the ages of non-harvested branches on the analyzed trees were not known, another regression was computed that related branch BD to age. Age estimates of each branch on each of the analyzed trees were then made.

"Other" branch wood and bark productivity estimates were made by subtracting from the estimated biomass of a branch the estimated biomass of a branch one year younger than the estimated age of the branch. Bole wood and bark productivity estimates were made using data obtained from analysis of tree cores. Ring width measurements for each core from each of the last ten years were averaged together for use in the productivity estimates. Wood productivity was considered to be the biomass of the hollow volume of wood with wall thickness equal to the thickness of the average yearly wood increment over the last ten years and outside diameter equal to the whole bole diameter minus that portion of the diameter attributable to the bark. Volume of the bole was again considered to be one-half of the basal area times the height. Conversion of volume to mass made use of the density values obtained from the tree cores. Bark productivity was estimated by dividing the total bark biomass by the age of the tree. Wood and bark productivity estimates were added together for each of the cored trees and regressed against the trees' DBH after the appropriate logarithmic transformations. Quadrat tree counts were translated into net primary productivity totals using the prediction equations. Values were expressed as $g/m^2/yr$.

Shrubs

Shrub productivity was estimated using a dimension analysis procedure similar to that used for tree species. Basal diameter tallies of shrubs were made in 3.1 m^2 quadrats centered on the centers of the 25 m^2 quadrats used for the trees. Regression prediction equations were developed only for *Vaccinium corymbosum* since it was the only shrub species that contributed substantially to the biomass or productivity. Nine randomly selected *Vaccinium* stems were chosen to represent the BD size distribution observed in the quadrat populations. These stems were harvested in early September by sawing them off at ground level. They were treated in the laboratory in the same manner as the tree branches had been treated. That is, they were oven-dried at 80°C and divided into leaves, current shoots, "other" wood and bark, and dead wood, before being weighed. Regression equations relating the logarithms of the stem BD to the logarithms of the various biomass and net primary productivity components were developed by the same method used for tree branches. Quadrat analyses of *Vaccinium* populations were used along with the prediction equations to estimate the biomass and productivity per unit area. In addition, an estimate of the *Vaccinium corymbosum* fruit production was made. This was done by collecting all of the fruit from 41 randomly selected stems during mid-July when the fruit was ripening. Fruit production on an areal basis was estimated by multiplying the average fruit production per stem by the average number of stems per unit area. *Vaccinium* prediction equations were used to estimate biomass and productivity of other shrub species as well.

Seedlings and Saplings

Biomass and productivity of seedlings and saplings of tree species was estimated using regressions constructed for estimating individual branch productivity of the trees. Saplings were considered to be individuals of tree species that were less than 137 cm but greater than 10 cm tall. Basal diameter tallies of saplings were made in the same 25 m^2 quadrats used for the larger trees. Seedlings were considered to be those individuals of tree species that were less than 10 cm tall. Quadrats used for basal diameter tallies of seedlings were 0.5 m^2 in size and centered on the same points as the 25 m^2 quadrats. The log of the BD values of the seedlings and saplings was used as the independent variable in place of the logarithm of the diameter at point of bole attachment used for branches of trees in the regression equations. *Picea* branch regressions were used for *Picea* seedlings and saplings while *Larix* regressions were used for all other species.

Sphagnum

Net primary productivity of the sphagnum mosses (Sphagnum spp.) was estimated using one of the methods detailed in Clymo (1970). The selected method involved the placement of crank-shaped wire reference markers in the Sphagnum mat. The markers were constructed from steel surveyor markers which in their unaltered state consisted of 0.91 m of 0.16 cm diameter steel wire with a colored plastic flag at one end. These markers were bent in two places to form the desired crank shape. This configuration of the wires provides a horizontal section that inhibits slippage through the peat. One hundred marker locations were randomly selected in the bog area in mid-April, 1978. Locations for placement of the markers were selected using a map of the area that did not precisely define the margins of the bog proper. Therefore, some of the locations chosen for placement of the markers were in areas outside of the true bog. In these locations, no markers were positioned. Markers were also not implanted in locations within the bog boundaries that lacked Sphagnum cover. Where the randomly selected points were found to be Sphagnum covered, a wire marker was inserted into the peat with the horizontal section of the marker parallel to the growth surface of the Sphagnum. After the wire was implanted, measurements were taken of the Sphagnum height abov e the horizontal portion of the marker. Measurements were made using a metal rule with an attached slide. Five measurements, equally spaced along the horizontal portion of the wire, were made at each marker. The bottom of the rule was placed in contact with the horizontal portion of the wire and the slide was then lowered to contact the surface of the growing *Sphagnum*. A total of 55 markers was placed in the peat. The five measurements from each marker were averaged together for later comparison with future measurements to determine *Sphagnum* growth. *Sphagnum* samples were taken in April and November near each marker for identification of the species present and determination of biomass values per unit length of growth. The first measurements of growth were obtained in mid-July. After the July measurements, the markers were repositioned randomly along the transect lines so that it was easier to locate them for the second set of measurements in mid-November. Linear growth estimates were multiplied times dry mass per unit length of stem and branches beneath the growth apex to obtain net primary productivity per stem. Mass per unit length values were obtained in the laboratory using the "capitulum correction" method recommended by Clymo (1970). This method corrects for changes in mass of the growing apex of the shoots from the beginning of the growth period to the end. It has been shown by Clymo that there is a fairly close relationship between the dry weight of the *Sphagnum* capitulum (defined for convenience as the top one cm of the plant) and that of a unit length of stem after the branches have been removed. Spring time capitulum masses were regressed against naked stem masses for later use. This relationship was used to predict what the spring capitulum mass of plants harvested in the fall had been. The difference between the fall and spring capitulum weights was then used to correct the weight loss or gain to the rest of the plant from the capitulum so that the final figure reflected true production for the period. Productivity results were converted to an areal basis using density data obtained from 0.1 m^2 quadrats centered on each of the *Sphagnum* markers in their original locations.

Herbs

Herb productivity was estimated using biomass per unit area data obtained through visual estimates of percent cover combined with sampling and weighing of the herb species present in the bog. Percent cover estimates for each of the species were made in 0.5 m^2 quadrats centered on the 25 m^2 quadrats used for the tree counts. Specimens of most of the herbaceous species were removed from the wooded area adjacent to the bog where they were more common than in the bog itself and showed no apparent differences in structure when compared to the bog plants. The sampled specimens were oven dried and weighed. Mass values per unit area of cover were calculated. These relationships were used to convert the visual estimates of percent cover from the bog into biomass figures. Net primary productivity was assumed to be equal to the early September standing crop.

RESULTS AND DISCUSSION

Trees and Shrubs

Tree and shrub biomass summaries are presented in Tables 1 and 2 respectively, while tree and shrub net primary productivity summaries are presented in Tables 3 and 4. In Appendix Tables A1 and A2 DBH values for all tallied trees and BD values for all tallied shrubs are found. Tables A3 and A4 contain dimension analyses of *Picea* and *Larix* trees. *Picea*, *Larix*, and *Vaccinium* sample branch component masses are listed in Tables A5, A6, and A7 respectively. Regressions used for estimating biomass and productivity of woody species are given in Tables A8, A9, and A10. Importance values for trees and shrubs are found in Tables A11 and A12 respectively.

Biomass accumulation ratios (biomass/net primary production) for the three major woody species in the Waterloo Bog were found to vary considerably. *Picea mariana*, *Larix laricina*, and *Vaccinium corymbosum* were found to have biomass accumulation ratios of 9.1, 16.9, and 2.8 respectively. The difference between *Picea* and *Larix* could be largely attributable to a marked difference in population size structure. Figures 4 and 5 illustrate these population structures.

Table 1

Aboveground tree biomass. (g/m^2; includes seedlings and saplings)

SPECIES	DEAD WOOD	LEAVES	CURRENT SHOOTS	"OTHER" BRANCH WOOD AND BARK	BOLE WOOD AND BARK	TOTAL
Picea mariana	172	242	17	285	881	1597
Larix laricina	769	38	5	594	2648	4054
Acer rubrum	10	2	1	12	32	57
TOTAL	951	282	23	891	3561	5708

Table 2

Aboveground shrub biomass. (g/m^2)

SPECIES	DEAD WOOD	LEAVES	CURRENT SHOOTS	"OTHER BRANCH WOOD AND BARK	FRUIT	TOTAL
Vaccinium corymbosum	32	269	46	1066	2	1415
Other*	-	-	-	-	-	5
TOTAL						1420

*Subtotals not included in table.

Table 3

Aboveground tree net primary productivity. ($g/m^2/yr$).

SPECIES	LEAVES	CURRENT SHOOTS	"OTHER" BRANCH WOOD AND BARK	BOLE WOOD AND BARK	TOTAL
Picea mariana	46	17	45	65	173
Larix laricina	37	5	120	55	217
Acer rubrum	2	0	5	2	9
TOTAL	85	22	170	122	399

Table 4

Aboveground shrub net primary productivity. ($g/m^2/yr$).

SPECIES	LEAVES	CURRENT SHOOTS	"OTHER" BRANCH WOOD AND BARK	FRUIT	TOTAL
Vaccinium corymbosum	269	46	191	2	508
Other*	-	-	-	-	1
TOTAL					509

*Subtotals not included in table.

Larix can be seen to have a much more mature population with fewer young individuals than *Picea*. Also, many of the *Larix* trees apparently had large numbers of their leaf buds destroyed early during the 1978 growing season, possibly the work of larch sawflies. All components of production may have been affected by the loss but leaf and current shoot production would show the greatest response since their estimates are based on only the current year's production. *Vaccinium*'s relatively low biomass accumulation ratio is largely due to the fact that shrubs tend to accumulate less biomass than do trees (Whittaker and Likens, 1975).

Figure 5 presents the ages of cored *Larix* and *Picea* trees versus their DBH values. There is an overall trend for *Larix* to be somewhat larger at a given age although there is a good deal of overlap in their distributions. A regression of age versus DBH yields a predicted value of 14.0 cm DBH for *Larix* and 10.8 cm DBH for *Picea* at an age of 50 years. Fowells (1965) relates growth information on *Picea* and *Larix* under varying site conditions. Under optimal conditions, a specimen of *Larix laricina* may reach a height of 60 feet and a DBH of 18 inches in 45 years. In certain stagnant swamps, *Larix* grows slowly and may be only six feet tall in 55 years. *Picea mariana* under very poor conditions may be only one or two inches in diameter and 10 to 20 feet tall when 100 to 200 years old. Apparently the Waterloo Bog represents a site of moderate quality

Figure 4

<u>Picea</u> <u>mariana</u> DBH distribution

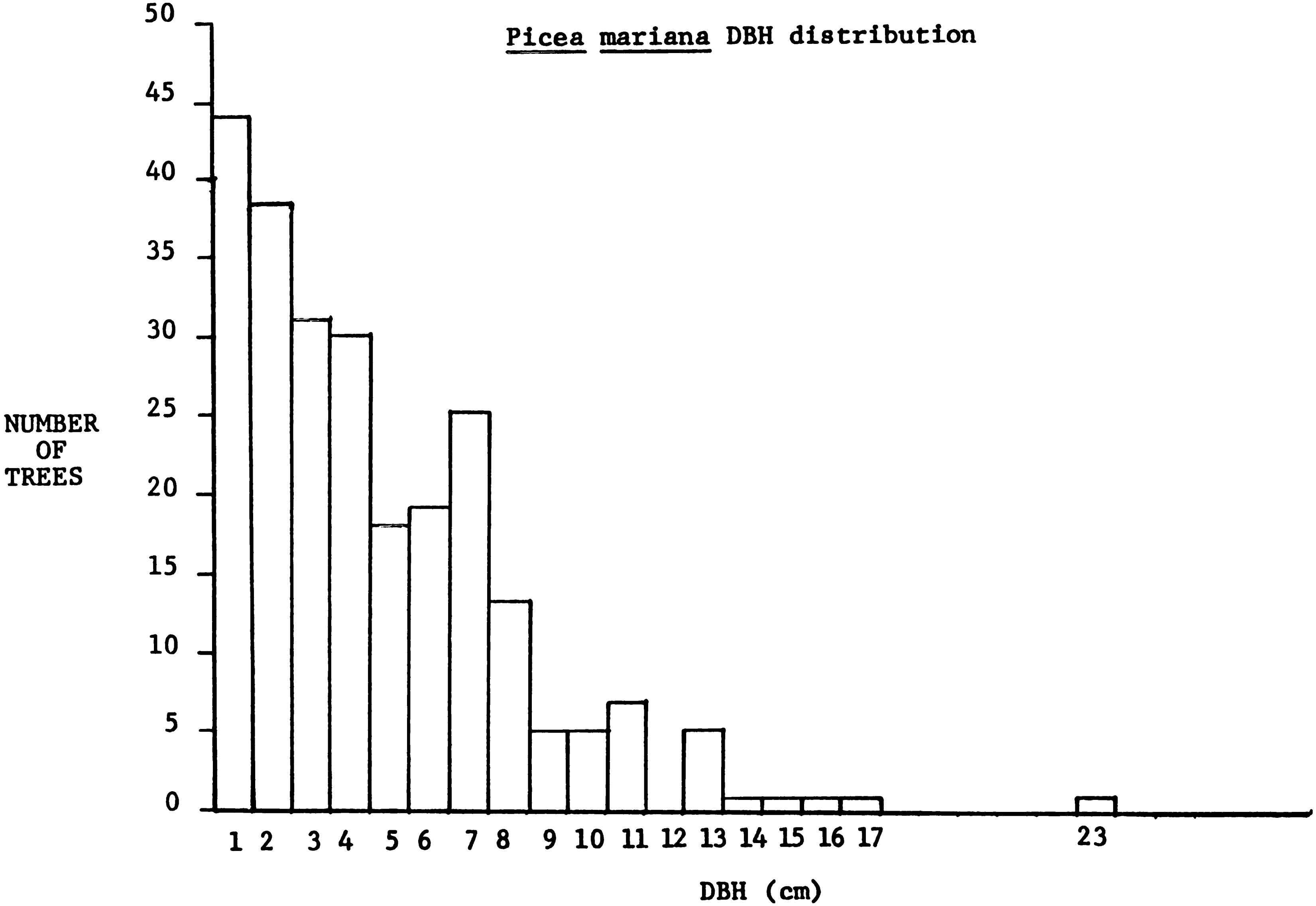


Figure 5

Larix laricina DBH distribution

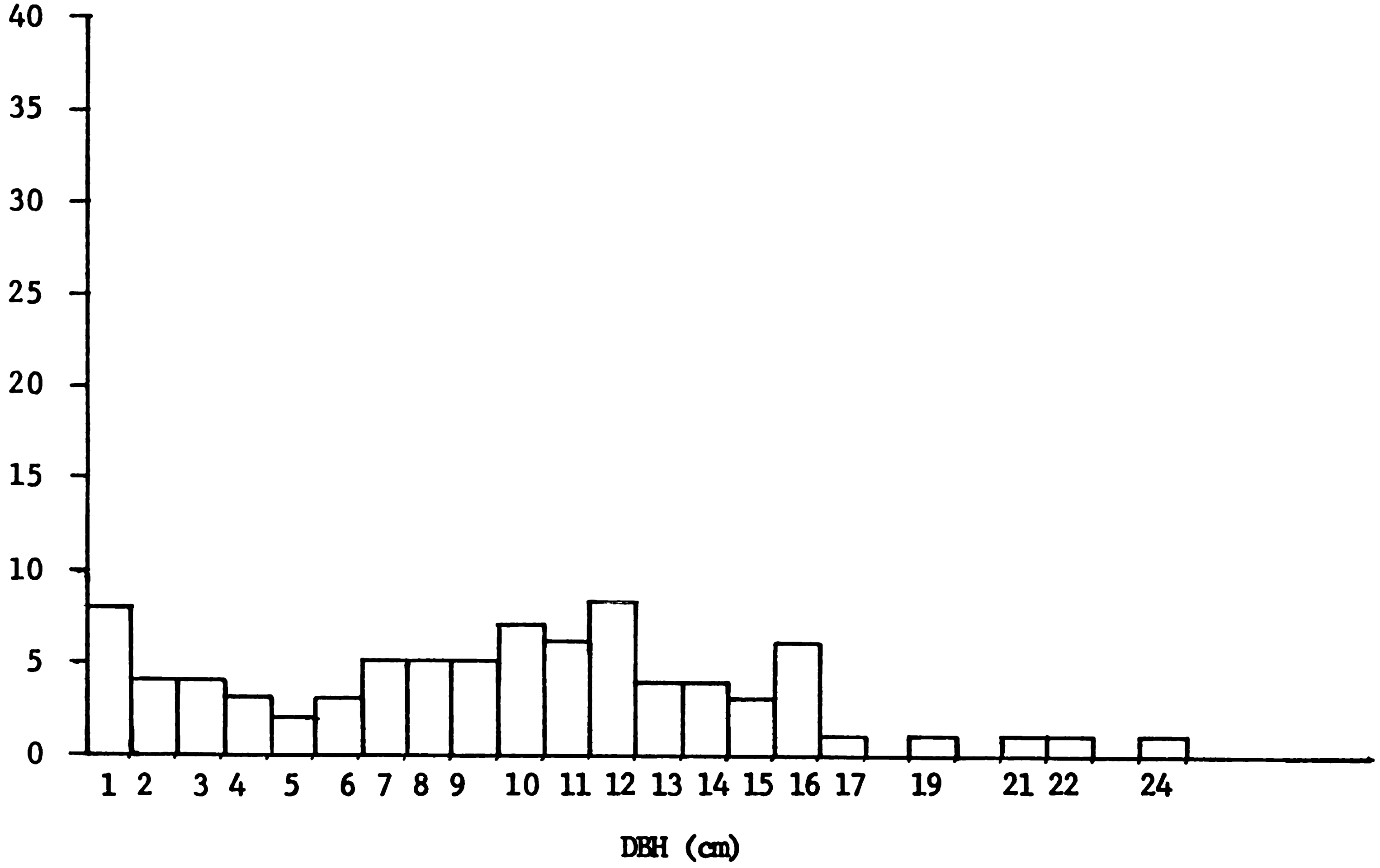
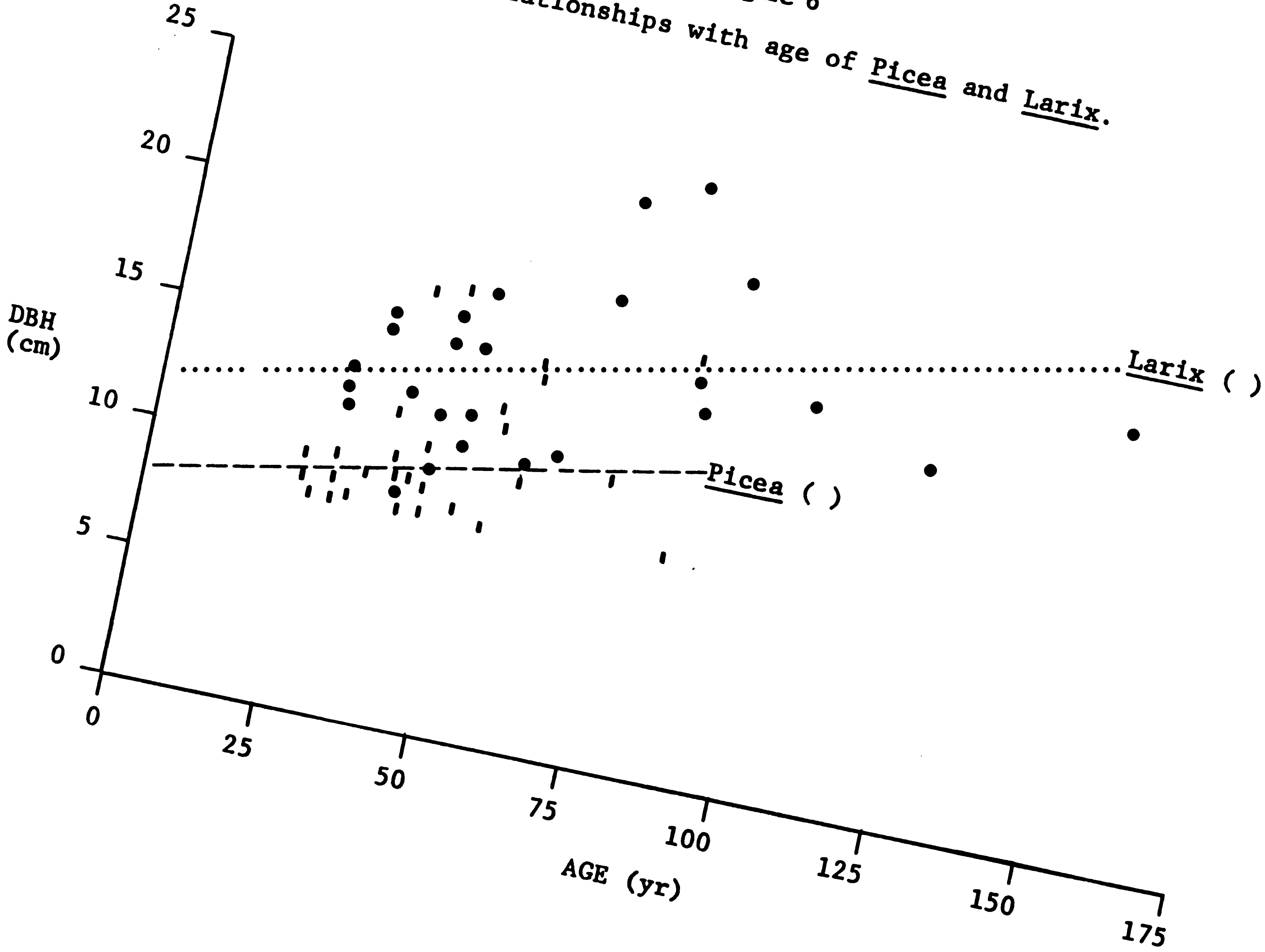


Figure 6

DBH relationships with age of <u>Picea</u> and <u>Larix</u>.



for the growth of both *Picea* and *Larix*. In the study area, both species are near the southern limit of their ranges. Both range over most of Canada, interior Alaska, and the extreme northern sector of the eastern United States. In southern Michigan, both are confined almost exclusively to bogs. This restriction to bogs may be largely due to their inability to compete with other species on more favorable sites since both apparently grow better on mineral soils than on the sphagnum soils when competition is not a factor (Fowells, 1965). *Larix* is especially intolerant of competition and cannot become established in shade. *Picea* is somewhat more shade tolerant and may develop with as little as 10 percent of full sunlight intensity.

There are a number of problems inherent in the dimension analysis procedure for estimation of plant biomass and productivity. For one thing, the logarithmic regressions have characteristics that make it difficult to express error and confidence limits in concise forms. It is not generally possible to establish standard deviations for results due to possible violation of certain assumptions necessary for calculations of these statistics. The method used to estimate production of branch wood and bark of trees and stem wood and bark of shrubs in this study apparently tends to overestimate these values (Whittaker, 1965). This overestimation may be due to a higher death rate for smaller branches of a given age category. There is a need for more studies to compare more direct estimates of productivity with productivity estimates obtained through dimension analysis. This would help to establish sources of error and methods for their correction.

Neglect of herbivory and litter drop of current year's production probably did not introduce any serious error to the Waterloo Bog productivity estimates. In forests the fraction of aboveground net production harvested by insects, the major consumers, generally amounts to less than 3 percent of the total aboveground production (Whittaker and Marks, 1975).

Sphagnum

Sphagnum spp. growth and productivity data is summarized in Table 5.

According to Clymo (1970), reported values for Sphagnum productivity vary from 77 g/m^2/yr to 166 g/m^2/yr. The 98 g/m^2/yr for the Waterloo Bog puts this Sphagnum carpet in the low productivity range. Of the total 3.01 cm average growth for Sphagnum in the Waterloo Bog, 2.59 cm occurred in the April to July growth period while only 0.42 cm of growth occurred in the July to November growth period. This reduction in growth was probably largely attributable to the seasonal lowering of the water table which caused many of the Sphagnum plants to become

Table 5

Sphagnum growth and productivity

SPECIES	% COVER	GROWING TIPS PER m^2 AT FULL COVERAGE	GROWTH (cm) APRIL-JULY	GROWTH (cm) JULY- NOV.	g/cm GROWTH	BIOMASS (g/m^2) OR NET PRIMARY PRODUCTIVITY ($g/m^2/yr$)
Sphagnum magellanicum	35.6	9000	-	-	.0043	-
Sphagnum recurvum	47.3	12600	-	-	.0025	-
Sphagnum subnitens	3.1	32000	-	-	.0022	-
AVERAGE	-	11800*	2.59*	.42*	.0032*	97.7
TOTAL	86.0	-	-	-	-	-

*Values are weighted to reflect relative coverages of species.

deleteriously dry. Increased shading by vascular plants during the second growth period may or may not have been important in affecting the growth of those *Sphagnum* plants that still had an adequate water supply. This strong seasonal decline in *Sphagnum* growth probably did not occur in the early stages of the bog's development when a floating mat was present. A floating mat is responsive to a certain extent to water table fluctuations and provides a more constant moisture regime for plants growing on its surface. It would be interesting to determine if *Sphagnum* species present on grounded areas are more resistant to periodic desiccation than are those species peculiar to the floating mat.

All three *Sphagnum* species showed a wide variability in growth from marker to marker. With the number of markers used it was not possible to detect any significant differences in growth rate between the species. This was partially due to the fact that many of the markers were in clumps that contained two or all three of the species. It may have been desirable to have an increased number of markers, especially in monospecific clumps, to obtain a better estimate of overall productivity as well as differences in growth of the three species. It is possible that a portion of the growth of the *Sphagnum* was missed since the markers were not implanted until mid-April and days suitable for *Sphagnum* growth occurred prior to this. Markers were not implanted this date so that any rebound of compaction due to snow melt would not be counted as growth.

The method used to measure Sphagnum growth did not appear to have any major shortcomings for use in the Waterloo Bog. It was easy to apply and did not have any readily apparent sources of error. Clymo (1970) voiced concern over whether the markers would slip relative to the peat and whether the presence of the markers would cause any changes in the growth of the Sphagnum. However, he observed no decrease of growth around the wires in four years of use of this method. Agreement of results obtained using the wire markers with results obtained using other methods tends to support the assumption that there is no slippage of the markers although there has been no direct test for this slippage.

Herbs

Estimates of biomass and productivity of herbaceous species are presented in Table 6. These estimates are admittedly of poor quality but should not affect the overall estimates of biomass and productivity since they represent only minute fractions of these quantities.

General Discussion

Results indicate that the Waterloo Bog is an area which compares favorably in productivity with other temperate zone ecosystems. The grand total 1007 $g/m^2/yr$ aboveground net primary production figure derived for the Waterloo Bog does not include belowground productivity. If this quantity was available to add to the aboveground figure, the total bog net primary productivity could possibly equal or surpass the figure of 1300 $g/m^2/yr$ given for an average temperate evergreen forest by Whittaker and Likens (1975). The same paper gives average net primary productivity values of 400 $g/m^2/yr$ for lakes and streams, 600 $g/m^2/yr$ for temperate grassland, 800 $g/m^2/yr$ for boreal forest, 1200 $g/m^2/yr$ for temperate deciduous forest, and 3000 $g/m^2/yr$ for swamps and marshes.

Forrest (1971) reported a total net primary productivity of 635 $g/m^2/yr$ for a British blanket bog. The aboveground portion of this productivity amounted to 407 $g/m^2/yr$. This was a dwarf shrub-tussock community dominated by *Calluna vulgaris* and *Eriophorum vaginatum*. Productivity of vascular plants was estimated using a peak biomass method combined with litter collection. Productivity of the *Sphagnum* mosses, which covered only about 15 percent of the area, was derived from previous work that used the same method employed in the Waterloo Bog. The topography of the

Table 6

Aboveground herb biomass and productivity

SPECIES	% COVER	g/m^2 AT 100% COVER	BIOMASS (g/m^2) OR PRODUCTIVITY ($g/m^2/yr$)
Drosera rotundifolia	0.04	2.43	0.10
Coptis trifolia	0.01	0.71	0.01
Maianthemum canadense	0.05	2.20	0.10
Vaccinium macrocarpon	0.02	5.00	0.08
Sedges and rushes	0.09	1.71	0.15
Cypripedium acaule	0.01	2.20*	0.02
TOTAL			0.46

**Maianthemum* value used for *Cypripedium*.

immediate area of the estimate consists of a low rounded hill. Peat depth was only 1.5 to 2.0 m.

Forrest and Smith (1974) expanded the work of Forrest to include a number of other blanket bog types in the same general area. Their productivity estimates were on seven sites within 1.6 km of the original site. Total net primary productivity ranged from about 500 to 900 g/m^2/yr. The mean was 659 g/m^2/yr.

Reader and Stewart (1972) obtained estimates of from 343 to 1026 g/m^2/yr aboveground net primary productivity for four contiguous peat accumulating areas in southeastern Manitoba. Including belowground estimates, productivity ranged from 710 to 1630 g/m^2/yr. From their site descriptions, the area they termed muskeg appeared to have a vegetation most similar to that of the Waterloo Bog. Their muskeg was occupied by widely spaced black spruce with ericaceous shrubs filling in the spaces. Ground cover was largely Sphagnum and Polytrichum mosses. This area had a total net primary productivity of 993 g/m^2/yr of which 326 g/m^2/yr was aboveground.

The 7277 g/m^2 biomass of the Waterloo Bog is an intermediate value when compared to other temperature systems. Lake and stream average biomass is only around 100 g/m^2 while temperate evergreen forest averages around 35,000 g/m^2 according to Whittaker and Likens (1975). Aboveground biomass accumulation ratios for all species in the Waterloo Bog was 6.9. This again is an intermediate value for a temperate system and reflects the degree of woodiness of the system. Biomass accumulation ratios in the systems studied by Forrest (1971), Forrest and Smith (1974), and Reader and Stewart (1972) ranged from 1.3 to 9.8.

From the findings in the Waterloo Bog and certain of the other boggy areas, it is evident that not all of these systems are of extremely low productivity. This is somewhat surprising in view of the extreme conditions for plant life found in these habitats. Plants found in bogs must be able to cope with a high and variable water table, limiting supplies of nutrients and low pH values within which few plants can survive and under which even fewer plants are capable of producing biomass at their maximum rate. On the other hand, bog plants are seldom subjected to an inadequate moisture supply which is a major factor limiting productivity in many other ecosystems. Also, the low pH value of the sphagnum peat soils may not be as deleterious as the same low pH values on mineral soils. According to Lucas and Davis (1961), the optimum pH for maximum nutrient availability in sphagnum peats is around pH 5.0. This is about 1.5 pH units below that pH generally considered to be most desirable for mineral soils.

It would be interesting to know the belowground biomass and productivity of the Waterloo Bog. However, root productivity estimation methods are of a much more primitive nature than are shoot methods. This is largely due to the inaccessibility of the roots. Also, wood rings and consequently ages are probably more uncertain in roots than in branches. Most estimates of root production make use of the assumption that the ratio of production to mass is similar for the root and shoot systems. However, this assumption has not been proven and is likely false in at least some plants. Therefore, the validity of most estimates of belowground productivity is questionable and the lack of these data from the Waterloo Bog is perhaps less significant. Reader and Stewart (1972) in their study found that annual subsurface biomass and productivity were greatest in the treeless bog zone and least in the heavily wooded bog forest. They attributed this to the greater need for aerial biomass when there is competition among plants for sunlight. If this relationship holds for the Waterloo Bog, it should have a moderately low belowground biomass due to its moderate degree of shading. The values of Reader and Stewart (1972) from Manitoba for percentage of biomass and production belowground ranged from 84 percent for their bog to 42 percent for their lagg. Whittaker and Marks (1975) state that an average of 15 to 20 percent of total productivity in forests is attributable to roots.

Productivity for the Waterloo Bog is probably higher now than during earlier stages of its development. This may be deduced from several developments over the course of the bog's history. For one thing, there is probably more nutrient cycling occurring within the bog than there was during early stages of its development. The basin now is essentially filled in and it is doubtful that the peat level will rise much further under present conditions. This is because peat must be submersed beneath stagnant water to avoid decomposition. However, most of the bog surface currently is above the water table most of the year. Under these conditions, relatively little of the newly produced litter is preserved. During earlier developmental stages, much of the litter was deposited under water where decomposition was extremely slow. More recently, the increased decomposition should lead to increased nutrient cycling which should in turn tend to promote higher productivity. The arrival of agriculture to the area has also probably contributed to a rise in the Waterloo Bog productivity. Crop fields are found on three sides of the bog with only a narrow buffer zone of forest between the bog and the fields. There is probably a significant input of fertilizer-laden dust into the bog during spring, summer, and fall. This is probably especially true during times of plowing, harvesting, and cultivation of the cropland. It is also possible that there may be some surface runoff of nutrient enriched water from the fields into the bog during the spring thaw or during heavy rainstorms. There is a marked slope towards the bog from a cornfield on the eastern side. The southern portion of the natural area is not protected from incursion of the runoff by the drainage ditches mentioned earlier since these separate only the northern portion of the natural area from the fields. The soil of the fields is very sandy and likely has a high permeability which may limit the amount of runoff. Also, relatively little of what runoff there is may traverse the forest border to the bog. Since man has cleared much of the originally forested land in the area, the Waterloo Bog is one of the few remaining refuges for birds and mammals of the region. Many of these may provide a net nutrient input into the bog. Deer may be especially important in this regard since they probably do much of their feeding in the croplands and fields but take shelter and leave much of their feces in the bog. Numerous deer droppings are evident in the bog, especially during the early spring. Food remains from hawks were also noted on several occasions. The increase is productivity due to any of the above factors is not known but any or all of them may have a significant effect.

In order to gain a clearer understanding of bog dynamics, productivity should be combined with decomposition rates as well as with data dealing with rates of biomass and nutrient exchange with other systems. However, few data exist pertaining to rates of decomposition and nutrient cycling. Reader and Stewart (1972) estimated that, on the average, less than 10 percent of the net primary productivity will remain as peat. They found that about 25 percent of the net primary produc tivity will be lost in the first year. However, their direct experimental decomposition data were all from only the first year following litter fall. Additional decomposition rate estimates made use of C^{14} dating of lower strata combined with the assumption that productivity has been approximately constant through time. Obviously, this assumption could likely be false and their rates of decomposition inaccurate. Clymo (1965) experimented with the rates of _Sphagnum_ breakdown at different levels in the peat and found that decomposition dropped off sharply beneath the water level. He also found that certain _Sphagnum_ species are much more resistant to decay than others. Obviously, there is a need for much more good data on this subject, especially pertaining to decay rates at different stages of bog development.

There is an apparent need for a great deal more research into the subjects of productivity, decomposition, and nutrient cycling in bogs. Data are especially needed concerning how these factors interact as a bog matures from an open body of water to a fully grounded mat and beyond. Without such information it is not possible to fully appreciate the dynamics of these systems and predict their future successional development.

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APPENDIX

Table A1

Distribution of trees within DBH classes

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Picea mariana	49	38	31	30	18	19	25	13	5	5	7	0	5	1	1	1	1	0
Larix laricina	8	4	4	3	2	3	5	5	5	7	6	8	4	4	3	6	1	0
Acer rubrum	19	11	6	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0

	DBH (cm)					
SPECIES	19	20	21	22	23	23
Picea mariana	0	0	0	0	0	1
Larix laricina	1	0	1	1	0	1
Acer rubrum	0	0	0	0	0	0

Table A2

Distribution of shrubs within BD classes

	BD CLASS (cm)													
SPECIES	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8
Vaccinium corymbosum	810	19	35	71	31	53	66	34	26	15	29	30	11	17
Toxicodendron vernix	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Ilex verticillata	0	0	0	0	1	2	2	0	2	0	1	0	0	0
Nemopanthus mucronatus	0	2	1	3	1	1	1	0	1	2	0	1	1	3

	BD CLASS (cm)													
SPECIES	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0	3.2	3.6
Vaccinium corymbosum	16	17	10	8	8	13	10	8	8	0	3	1	1	2
Toxicodendron vernix	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Ilex verticillata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemopanthus mucronatus	0	0	3	0	1	0	0	0	0	0	0	0	0	0

Table A3

Branch tallies by BD classes for *Picea mariana*

BRANCHES	<0.3	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5
Tree 1 live	24	2	9	12	10	3	2	0	0	0	0	0	0	0
Tree 1 dead	22	2	1	1	0	0	0	0	0	0	0	0	0	0
Tree 2 live	17	7	9	10	5	7	1	1	0	0	0	0	0	0
Tree 2 dead	41	6	7	2	0	1	0	0	0	0	0	0	0	0
Tree 3 live	45	3	12	10	13	14	3	1	1	1	0	0	0	0
Tree 3 dead	29	0	0	5	2	0	1	1	0	0	0	0	0	0
Tree 4 live	12	6	15	7	14	12	7	14	6	4	2	0	0	0
Tree 4 dead	24	2	7	4	2	0	4	0	0	1	2	1	1	0
Tree 5 live	21	2	11	5	14	4	14	13	8	7	2	3	0	0
Tree 5 dead	59	5	28	18	6	10	7	3	2	1	0	0	0	0
Tree 6 live	37	0	6	4	4	5	7	2	1	2	2	0	0	0
Tree 6 dead	23	3	12	8	8	8	4	6	4	2	0	0	0	0
Tree 7 live	4	1	8	5	5	7	8	7	6	6	5	3	2	3
Tree 7 dead	14	2	5	1	8	4	7	17	9	3	2	4	4	4
Tree 8 live	10	4	8	5	8	5	8	4	7	5	0	2	1	0
Tree 8 dead	12	0	8	12	14	12	16	17	10	19	5	4	1	0
Tree 9 live	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 9 dead	0	0	0	0	0	1	2	1	1	2	0	3	2	2
Tree 10 live	4	8	6	6	7	8	7	11	7	5	4	2	8	4
Tree 10 dead	14	2	5	1	9	7	7	19	13	6	2	5	6	8

Table A3 (cont'd)

	BD (cm)										
BRANCHES	3.0	3.1	3.2	3.3	3.4	3.5	3.8	4.5	4.8	5.3	5.7
Tree 1 live	0	0	0	0	0	0	0	0	0	0	0
Tree 1 dead	0	0	0	0	0	0	0	0	0	0	0
Tree 2 live	0	0	0	0	0	0	0	0	0	0	0
Tree 2 dead	0	0	0	0	0	0	0	0	0	0	0
Tree 3 live	0	0	0	0	0	0	0	0	0	0	0
Tree 3 dead	0	0	0	0	0	0	0	0	0	0	0
Tree 4 live	0	0	0	0	0	0	0	0	0	0	0
Tree 4 dead	0	0	0	0	0	0	0	0	0	0	0
Tree 5 live	0	0	0	0	0	0	0	0	0	0	0
Tree 5 dead	0	0	0	0	0	0	0	0	0	0	0
Tree 6 live	0	0	0	0	0	0	0	0	0	0	0
Tree 6 dead	0	0	0	0	0	0	0	0	0	0	0
Tree 7 live	0	0	0	0	0	0	0	0	0	0	0
Tree 7 dead	0	0	0	0	0	0	0	0	0	0	0
Tree 8 live	0	0	0	0	0	0	0	0	0	0	0
Tree 8 dead	0	0	0	0	0	0	0	0	0	0	0
Tree 9 live	0	0	0	0	0	0	1	1	1	0	1
Tree 9 dead	0	0	0	0	0	0	0	0	0	0	0
Tree 10 live	0	0	0	0	0	1	0	0	0	0	0
Tree 10 dead	1	0	0	0	0	0	0	0	0	1	0

Table A3 (cont'd)

	BD (cm)													
BRANCHES	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9
Tree 1 live	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 1 dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 2 live	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 2 dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 3 live	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 3 dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 4 live	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 4 dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 5 live	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 5 dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 6 live	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 6 dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 7 live	4	1	1	0	0	0	0	0	0	0	0	0	0	0
Tree 7 dead	2	0	2	0	0	0	0	0	0	0	0	0	0	0
Tree 8 live	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 8 dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 9 live	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Tree 9 dead	1	1	1	0	1	0	1	0	0	0	0	0	0	0
Tree 10 live	1	1	0	0	2	0	0	1	0	1	0	0	0	0
Tree 10 dead	2	0	5	0	1	1	0	0	0	4	1	1	0	0

Table A4

Branch tallies by BD classes for *Larix laricina*

	BD (cm)														
BRANCHES	<0.3	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6
Tree 1 live	0	0	0	0	1	0	0	1	2	0	1	0	0	0	0
Tree 1 dead	2	0	2	2	1	0	2	0	0	0	0	0	0	0	0
Tree 2 live	34	6	27	7	3	0	1	2	3	1	1	0	0	0	0
Tree 2 dead	12	2	9	10	4	3	8	14	7	2	1	0	0	0	1
Tree 3 live	159	2	30	23	15	10	7	7	2	4	2	1	2	3	2
Tree 3 dead	16	4	2	3	3	1	0	3	2	2	1	1	2	1	0
Tree 4 live	342	13	99	52	33	21	16	19	3	0	0	6	0	14	0
Tree 4 dead	23	3	0	1	0	0	2	1	1	3	3	3	0	2	1
Tree 5 live	297	8	46	14	23	2	1	1	3	2	4	4	6	4	4
Tree 5 dead	22	2	4	2	0	5	3	2	2	4	5	6	3	2	3

	BD (cm)														
BRANCHES	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0	5.1
Tree 1 live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 1 dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 2 live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 2 dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 3 live	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 3 dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree 4 live	2	9	0	9	0	0	5	0	3	1	0	2	0	1	1
Tree 4 dead	2	2	0	1	1	1	0	0	0	0	0	0	0	0	0
Tree 5 live	4	1	1	0	3	1	5	2	0	0	1	0	0	1	0
Tree 5 dead	3	1	1	1	1	2	0	0	1	0	0	0	0	1	0

Table A5

Picea **mariana** sample branch dry weights.

BRANCH NUMBER	BD	AGE	DEAD WOOD	LEAVES ON CURRENT SHOOTS	LEAVES ON OLD SHOOTS	OLD WOOD AND BARK	CURRENT SHOOTS
1	<0.3	3	0	0.36	0	0.04	0.03
2	<0.3	4	0	0	0.19	0.19	0
3	<0.3	3	0	0.05	0.37	0.16	0.02
4	<0.3	3	0	0.23	0.62	0.28	0.04
5	<0.3	3	0	0.04	0.11	0.05	0.01
6	<0.3	7	0	0.26	1.16	0.45	0.04
7	<0.3	4	0	0.15	0.56	0.21	0.05
8	0.3	8	0.05	0.11	0.80	0.85	0.02
9	0.4	6	0	0.25	1.10	0.48	0.04
10	0.4	5	0	0.66	1.38	0.84	0.19
11	0.4	2	0	0.96	0.29	0.60	0.61
12	0.4	5	0	0.46	1.13	0.72	0.09
13	0.4	5	0	0.76	1.25	0.67	0.14
14	0.5	3	0	0.81	0.10	0.20	0.15
15	0.5	3	0	0.79	0.20	0.26	0.32
16	0.5	6	0	0.03	3.79	2.62	0.02
17	0.5	6	0.07	0	1.95	2.22	0
18	0.5	9	0	0.78	3.52	2.05	0.10
19	0.5	6	0	0.07	0.94	0.57	0.01
20	0.6	13	0.76	0.06	1.29	4.39	0.02
21	0.7	11	0	2.01	3.18	4.85	0.54
22	0.7	9	0.14	3.14	6.57	8.35	0.75
23	0.7	6	0.03	0.47	7.27	8.53	0.13

Table A5 (cont'd)

BRANCH NUMBER	BD	AGE	DEAD WOOD	LEAVES ON CURRENT SHOOTS	LEAVES ON OLD SHOOTS	OLD WOOD AND BARK	CURRENT SHOOTS
24	0.7	12	1.10	0.67	3.00	7.56	0.11
25	0.7	15	0.68	1.18	4.70	14.20	0.26
26	0.7	11	0.49	0.53	4.68	10.61	0.10
27	0.7	9	0	2.68	8.08	5.06	0.46
28	0.8	12	0.24	1.89	4.68	11.86	0.50
29	0.9	12	1.45	1.01	6.47	11.12	0.20
30	0.9	14	0.21	6.36	23.86	26.03	0.99
31	0.9	7	0	3.82	6.01	6.40	0.93
32	0.9	9	0.60	0.38	12.01	11.14	0.06
33	1.0	7	0	4.46	15.58	20.26	1.24
34	1.0	14	2.33	3.41	11.88	23.58	0.92
35	1.1	16	0.89	5.00	14.89	41.67	1.00
36	1.2	18	7.32	3.10	21.73	79.10	0.71
37	1.2	15	1.60	12.85	51.38	42.43	1.87
38	1.2	11	0.13	3.49	24.00	27.76	0.57
39	1.3	17	30.63	19.32	97.97	128.53	4.22
40	1.7	15	19.09	26.66	57.15	82.80	6.28
41	1.7	12	5.75	34.09	125.20	142.18	7.52
42	1.7	14	15.55	8.95	55.23	137.15	1.99
43	2.0	15	12.78	22.49	120.58	228.92	5.52
44	2.1	21	87.67	19.27	90.25	247.24	3.90
45	3.5	10	0	201.10	412.17	555.64	53.76
46	4.5	13	26.62	51.26	304.46	434.56	10.05

Table A6

Larix laricina sample branch dry weights (gm)

BRANCH NUMBER	BD	AGE	DEAD WOOD	LEAVES	OLD BARK AND BARK	CURRENT SHOOTS
1	<0.3	1	0	0.02	0	0.01
2	<0.3	1	0	0.03	0	0.02
3	<0.3	1	0	0.01	0	0.01
4	<0.3	1	0	0.01	0	0.03
5	0.3	1	0	0.02	0	0.04
6	0.3	1	0	0.01	0	0.02
7	0.4	2	0	0.53	0.79	0.12
8	0.4	3	0	0.22	0.20	0.05
9	0.4	4	0	0.45	1.20	0.19
10	0.5	4	0	0.05	0.04	0.12
11	0.5	4	0	0.26	0.63	0.05
12	0.6	9	0.63	0.40	3.31	0
13	0.6	6	0	0.39	3.44	0.15
14	0.7	4	0	0.49	3.52	0.02
15	0.9	10	0	1.10	10.70	0.10
16	1.1	9	3.37	1.27	28.32	0.38
17	1.2	10	0	2.98	18.62	0.62
18	1.2	10	23.15	5.82	82.94	1.43
19	1.5	8	13.37	1.44	17.98	0.35
20	1.7	10	10.14	15.21	135.38	1.00
21	1.7	15	36.28	23.25	178.68	1.11
22	2.0	16	7.64	28.27	205.15	1.11
23	3.1	19	55.14	34.06	643.55	5.33

Table A7

Vaccinium corymbosum sample stem dry weights (gm)

STEM NUMBER	BD	AGE	DEAD WOOD	LEAVES	OLD WOOD AND BARK	CURRENT SHOOTS
1	0.3	2	0.01	0.27	1.22	0.10
2	0.4	2	0.12	0.99	1.85	0.57
3	0.5	3	0.11	1.05	1.80	0.30
4	0.6	3	0.11	4.32	7.69	0.60
5	0.6	3	0.24	2.07	5.78	0.42
6	0.6	4	0.27	3.67	0.64	0.98
7	0.8	8	1.33	13.43	48.81	2.02
8	1.3	10	0.88	18.86	79.33	5.82
9	2.1	17	20.82	97.53	574.47	20.82

Table A8

Picea mariana regressions

INDEPENDENT VARIABLE(x)	DEPENDENT VARIABLE(y)	INTERCEPT (a)	SLOPE (b)	R^2
BRANCH BD	BRANCH AGE	1.021	0.600	.78
BRANCH AGE	OTHER BRANCH WOOD AND BARK	-2.523	3.592	.86
BRANCH BD	DEAD WOOD ON LIVING BRANCHES	0.075	3.292	.81
BRANCH BD	OLD LEAVES	1.175	2.353	.91
BRANCH BD	NEW LEAVES	0.560	2.153	.80
BRANCH BD	CURRENT SHOOTS	0.128	2.164	.83
BRANCH BD	OTHER BRANCH WOOD AND BARK	1.288	2.971	.93
TREE DBH	DEAD WOOD ON BRANCHES	0.902	1.268	.84
TREE DBH	OLD LEAVES	2.264	0.828	.87
TREE DBH	NEW LEAVES	1.709	0.737	.87
TREE DBH	CURRENT SHOOTS	1.274	0.742	.87
TREE DBH	OTHER BRANCH WOOD AND BARK BIOMASS	2.201	1.117	.85
TREE DBH	OTHER BRANCH WOOD AND BARK PRODUCTIVITY	1.920	0.422	.78
TREE DBH	BOLE WOOD AND BARK BIOMASS	2.051	2.221	.94
TREE DBH	BOLE WOOD AND BARK PRODUCTIVITY	1.241	1.520	.63
TREE DBH	DEAD BRANCH BIOMASS	1.313	1.850	.97

Table A9

Larix laricina regressions

INDEPENDENT VARIABLE (x)	DEPENDENT VARIABLE (y)	INTERCEPT (a)	SLOPE (b)	R^2
BRANCH BD	DEAD WOOD ON LIVING BRANCHES	0.599	2.413	.83
BRANCH BD	LEAVES	0.211	2.991	.91
BRANCH BD	CURRENT SHOOTS	-0.526	1.991	.90
BRANCH BD	OTHER BRANCH WOOD AND BARK	1.090	4.142	.93
BRANCH BD	BRANCH AGE	0.848	1.184	.92
BRANCH AGE	OTHER BRANCH WOOD AND BARK	-2.814	4.286	.96
TREE DBH	DEAD WOOD ON LIVING BRANCHES	1.145	1.659	.97
TREE DBH	LEAVES	0.789	1.729	.96
TREE DBH	CURRENT SHOOTS	0.057	1.617	.98
TREE DBH	OTHER BRANCH WOOD AND BARK BIOMASS	1.500	2.118	.93
TREE DBH	OTHER BRANCH WOOD AND BARK PRODUCTIVITY	0.915	2.078	.93
TREE DBH	BOLE WOOD AND BARK BIOMASS	2.992	2.306	.96
TREE DBH	BOLE WOOD AND BARK PRODUCTIVITY	0.452	2.188	.72
TREE DBH	DEAD BRANCH BIOMASS	0.869	2.770	.92

Table A10

Vaccinium corymbosum regressions

INDEPENDENT VARIABLE(x)	DEPENDENT VARIABLE(y)	INTERCEPT (a)	SLOPE (b)	R^2
STEM BD	STEM AGE	0.853	1.208	.95
STEM AGE	OTHER WOOD AND BARK	-0.638	2.658	.98
STEM BD	DEAD WOOD	0.078	3.300	.95
STEM BD	LEAVES	1.110	2.929	.97
STEM BD	CURRENT SHOOTS	0.428	2.577	.97
STEM BD	OTHER WOOD AND BARK BIOMASS	1.653	3.341	.97
STEM BD	OTHER WOOD AND BARK PRODUCTIVITY	1.137	2.254	.97

Table A11

Tree importance values

SPECIES	DENSITY	RELATIVE DENSITY(RD)	FREQUENCY	RELATIVE FREQUENCY(RF)	IMPORTANCE VALUE(RD+RF)
Picea mariana	.31/m^2	67.4%	93.8%	45.5%	112.9
Larix laricina	.10/m^2	21.7%	87.5%	42.4%	64.1
Acer rubrum	.05/m^2	10.9%	25.0%	12.1%	23.0

Table A12

Shrub importance values

SPECIES	DENSITY	RELATIVE DENSITY(RD)	FREQUENCY	RELATIVE FREQUENCY(RF)	IMPORTANCE VALUE(RD+RF)
Vaccinium corymbosum	13.5/m^2	96.7%	97%	68.8%	165.5
Toxicodendron vernix	.05/m^2	.4%	13%	9.2%	9.6
Ilex verticillata	.11/m^2	.8%	9%	6.4%	7.2
Nemopanthus mucronatus	.30/m^2	2.1%	22%	15.6%	17.7