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THE WOOD AND BARK BIOMASS AND PRODUCTION OF *Populus tremuloides*, *Abies lasiocarpa* AND *Picea engelmannii* IN NORTHERN UTAH

by

George L. Zimmermann

A thesis submitted in partial fulfillment of
the requirements for the degree

of

MASTER OF SCIENCE

in

Forest Ecology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1979

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On a large project such as this there have been many people to help through the years. I'd like to thank them all.

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George Zimmermann

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ABSTRACT

The Wood and Bark Biomass and Production of

Populus tremuloides, Abies lasiocarpa, and Picea engelmannii

in Northern Utah

by

George Zimmermann, Master of Science

Utah State University, 1979

Major Professor: Dr. Jan A. Henderson
Department: Forestry and Outdoor Recreation

Thirty-two engelmann spruce (Picea engelmannii) ranging in d.b.h. from 9.4 to 84.6 cm, twenty subalpine fir (Abies lasiocarpa) with d.b.h.'s from 8.1 to 58.8 cm, and twenty aspen (Populus tremuloides) ranging in d.b.h. from 4.5 to 48.2 cm. were destructively sampled in Northern Utah to construct wood and bark biomass and production prediction equations for above and below ground parts. These prediction equations were then applied to stand table data from 20 x 25 meter plots representing a sere that changes from subalpine meadow to aspen to fir to a 'climax' stand of spruce. The biomass production data along the successional stages were then used to test some of Odum's hypotheses regarding ecosystem development (Science 1969).

In all biomass and production predictive equations diameter at breast height (1.38 meters) and its transformations was found to be the single best independent variable. Spruce bole bark biomass was

best correlated linearly with d.b.h. Spruce bole wood, branch wood and branch bark were best predicted with a d.b.h.^{2} relationship. All fir above ground biomass components as well as all aspen above ground components except aspen branch wood were best correlated with d.b.h.^{2} Aspen branch wood biomass was best predicted by a d.b.h.^{3} equation. Seedling sized fir, spruce, and aspen (trees less than 1.38 meters in height) had their total above ground wood and bark biomass best predicted using basal diameter^3 as the independent variable.

Seven spruce and fir stump and root systems, from trees ranging from 2.5 to 66.0 cm. in d.b.h., were excavated by hand. All roots down to one centimeter in diameter were cut weighed and oven-dried. Biomass data from the fir and spruce stumps and roots were combined because of their similarity. The resulting combined biomass data was described accurately by using d.b.h.^{4} as the independent variable. Aspen root biomass was obtained through the use of three randomly located excavated cubic meter pits in each of four different clones. The aspen pit root biomass was best described by employing a sixth degree polynomial using the diameter (cm) of the four nearest trees to pit center divided by their average distance (meters) to pit center.

Two production methods were used: 1) mean annual increment (MAI) and 2) periodic annual increment (PAI). No production estimates for roots were made. Spruce bole wood and bark MAI's were best predicted by d.b.h. and log-log d.b.h. equations respectively. Spruce branch wood and branch bark MAI's were both best described by d.b.h. (linear) relationships. All fir MAI branch and bole components used d.b.h.^{2} in their predictive equations. All aspen MAI equations used sixth degree polynomials with d.b.h. as the independent variable. Polynomials were employed when downward or leveling trends could not be adequately represented using standard statistical techniques.

Spruce and aspen PAI equations were constructed using polynomials. Fir PAI, because of the data, could be best predicted using standard regression techniques. Fir bole wood and bark PAI equations were linear and thus best described by d.b.h. untransformed. Fir branch and wood PAI showed some leveling which was gradual enough to best be fitted by a d.b.h.$^{.3}$ equation.

Using the biomass and production predictive equations and stand tables from plots representing a succession, plot biomass and productions were generated. The plot biomasses and productions were plotted against estimated age (time from the initial meadow invasion by aspen). Above and below ground total wood and bark plot biomass was found to increase with time through all stages being low in early aspen dominated stages (1.5×10^5 kg/ha @ 7.5 years) to high in late spruce dominated stands (5.25×10^5 kg/ha @ 258 years). This finding supports Odum's hypothesis that biomass is low in early stages and higher in later stages of ecosystem development.

Both estimates (MAI and PAI) of total above-ground plot production show that production is high in early aspen stages (PAI is 4.7×10^3 kg/ha/yr @ 65 years), low in mid-successional fir dominated stands (PAI is 3.0×10^3 kg/ha/yr @ 130 years), and high again in the late spruce stages (4.6×10^3 kg/ha/yr @ 258 years). This tends to contradict Odum's hypothesis that production tends to keep decreasing after the initial stages of succession. While these tests of Odum's hypotheses are only on the basis of tree wood and bark, these values will probably

be found to be the largest single biomass and possibly production community contributors.

(95 pages)

INTRODUCTION

Biomass is the weight of living organisms commonly expressed as an oven-dried weight per unit area (kg/ha). Production is the amount of biomass formed per unit time (kg/ha/yr). Though biomass studies can be traced back as early as the 1800's it has only been recently received a quantum leap in scientific efforts. Some of the motivation for biomass research has stemmed from pure scientific interest but in light of today's energy crisis such research takes on more important meaning.

Plants are essentially the only organisms on earth capable of naturally producing their own organic matter by utilizing solar energy and available minerals. Therefore, a knowledge about this indispensible plant resource base becomes crucial, especially in light of rising populations and the energy crisis. Plant biomass and production studies help to quantify this resource base and also give us an idea of energy capture and flow in natural communities. By quantifying our natural communities' energy capture and flow we come closer to knowing the natural resource limits we can exploit and grow under.

This study will present data on the biomass and production of three naturally occuring communities dominated by aspen, fir and spruce. Since these communities represent three of the four basic stages of a succession (the treeless subalpine meadow is the missing stage), we will be able to test some of Odum's hypotheses regarding ecosystem development (Science 1969). Until now tests of these hypotheses have been limited to the researcher's field of expertise (e.g., Nicholson and Mark 1974). This study is part of a larger NSF funded project designed to test eleven of Odum's hypotheses in light of all community components (from soil invertebrates to vertebrates to trees).

STUDY SITE

The study site was located in the Wasatch mountains in Northeastern Utah approximately 56 kilometers northeast of Logan, Utah at approximately $111^{0}29'$ longitude and $41^{0}53'$ latitude. The study area is represented by two replicates (A and B) of the same sere. Each replicate is divided into four successional stages. The stages correspond to meadow, aspen, fir and spruce (see Figure 1). Each stage is further subdivided into treatments that correspond to a level of predation from large grazing animals (sheep, cattle) to no herbivore consumption (the latter treatment being sprayed with Temec). For a diagram of the plots and study area see Figure 2.

The elevation of the study area ranges from 2530 meters to 2600 meters. The area is on a gentle north facing ridge. The climate is continental, having short dry summers and long cold winters. The precipitation at the site has been monitored by G. Hart and T. W. Daniel (1977) since the 1970 water year. For a comprehensive summary see Table 1.

Figure 1. Aerial photo of typical vegetation pattern in study area.

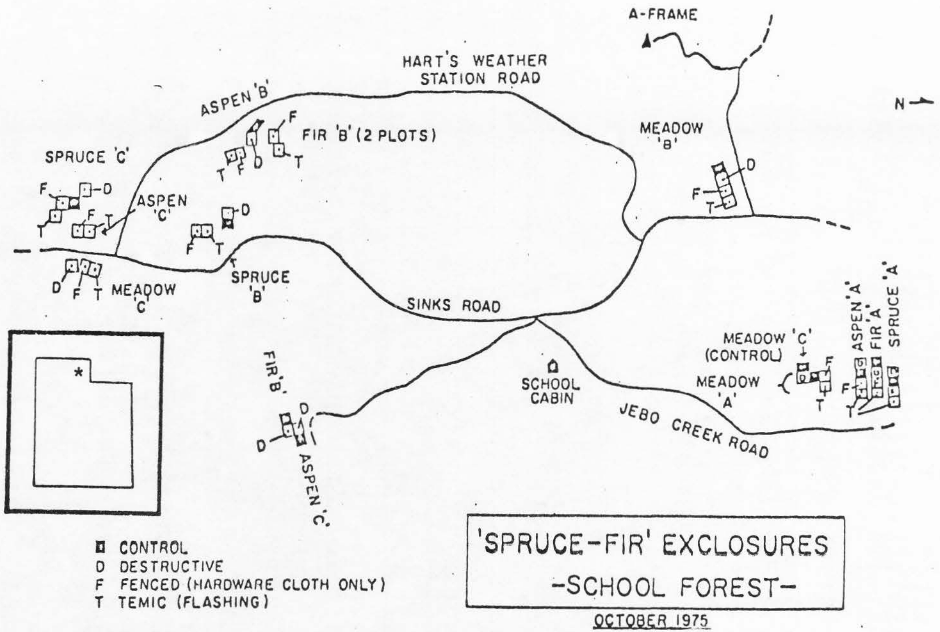


Figure 2. Diagram of location of study area and plots. Inset shows position of School Forest in Utah.

Table 1. Precipitation measured at study area (data is presented in inches of water).

Month	Water year precipitation						
	1970	1971	1972	1973	1974	1975	1976
	inches						
October	1.92	5.23	4.41	3.27	1.52	3.49	3.86
November	0.92	9.32	3.35	2.98	7.10	2.13	5.39
December	5.15	7.24	7.59	8.19	7.08	4.33	2.99
January	8.90	7.95	10.45	2.69	5.42	5.48	3.97
February	1.15	0.85	5.30	3.02	3.63	5.57	4.75
March	3.65	6.24	4.45	5.84	5.95	7.24	5.57
April	4.15	3.03	6.00	3.60	3.05	4.31	3.46
May	3.25	1.90	0.35	1.65	2.32	3.96	1.44
June	1.95	1.15	2.85	1.61	.85	2.55	1.46
July	0.72	0.48	0.00	1.45	1.37	.61	1.30
August	0.25	1.17	0.65	1.32	.33	.52	.71
September	1.65	1.79	2.45	2.77	.15	.58	1.12
TOTAL	33.66	46.35	47.85	38.44	38.77	40.77	36.02

OBJECTIVES

The objectives of this study are:

1. To construct wood and bark biomass predictive equations for above and below ground parts of aspen, fir and spruce.

2. To construct wood and bark production predictive equations for above ground parts of aspen, fir and spruce.

3. To apply the equations from the above objectives to plots representing a typical sere in Northern Utah in order to determine changes in wood and bark biomass and production through successional time.

4. To use all of the above information to test some of Odum's hypotheses regarding ecosystem development (Science 1969).

METHODS

The three basic approaches for estimating stand biomass and production are unit area, average tree, and regression analysis (or every tree summation, Baskerville 1965). The unit area approach involves destructively sampling trees on a particular area (e.g., a .1 hectare circular plot). The biomass and production estimates based on this plot are then multiplied by a suitable blow-up factor to arrive at stand biomass for the entire area (Ovington et al. 1968). When using average tree method (Ovington et al. 1959) a tree representative of some average dimension (e.g., d.b.h.) of the stand is selected. The tree is then biomassed and its value multiplied by the number of trees in the stand.

The third method involves destructively sampling a range of different sized trees. From these sample data regression equations are constructed to predict a tree's biomass on the basis of some easily measured parameter such as d.b.h.

These regression equations are then applied to every tree on the plot and the results summed. Based on various studies (Kittridge 1944, Ovington and Madgwick 1959, Baskerville 1965, Attiwill 1966, Ovington et al. 1968, Attiwill et al. 1968, Baskerville 1972) in which these different methods were analyzed, the regression analysis approach was found to be the most accurate. On this project the regression analysis method was used.

Our sampling methods were derived from Whittaker 1961, Whittaker and Woodwell 1968, and Newbould 1967.

In sampling trees either of two procedures ("extensive" or "intensive") were used. At first a few trees (usually three or four) were intensively sampled, that is, the trees were carefully sampled and broken into components of wood, leaves, and bark. From these trees regression equations were generated to be used in predicting component amounts on various parts of the extensively sampled trees (especially the branches). A more detailed description of intensive and extensive tree sampling is described later.

In all cases off-plot trees were sampled to represent as wide a variety of diameters as would be encountered on our plots. The sampled trees were chosen from areas representing the same habitat type as our study (target) plots (Henderson et al. 1976).

Individual Tree Estimation

Branches

For intensively sampled engelmann spruce the boles were first marked for true north. Extension ladders were then placed on the bole. As each branch was encountered it was sequentially numbered, its azimuth recorded, as was its height from the stump, total length, the diameter inside and outside the bark at the branch base, and its total green weight.

When every tenth branch on an intensive tree was encountered it was broken into categories and its components (leaves, wood and bark) sampled. The categories were generalized as the main branch, leafy twigs, leafless twigs and new growth. The main branch is defined as the primary section of the limb from its connection to the bole to the point where it loses its character (i.e., where it forks). The leafy twigs are those parts of the limb that are woody and possess leaves. Leafless twigs are those woody areas of the limb that have lost their leaves and are not part of the main branch. New growth is the current year's leaves and twig. It was found that new growth segments contained negligible wood and were primarily composed of bark and leaves. Samples were taken from each of the bark and leaf categories. Samples were usually at least 1 and not more than 10% by weight. For example, after dissecting a branch into its parts, 500 grams of leafy twigs might be taken from a particular branch, therefore between 5 and 50 grams would be randomly taken and stripped into their green components (wood, bark, and leaves), weighed and bagged (see Figure 3).

For the main branch a sample one decimeter long would be cut from the center of the branch. It was then separated into wood and bark, weighed green and bagged for dry weight determination in the lab. Small main branches were completely separated and bagged. The base of the main branch was also bagged for age and radial increment determination in the lab.

The branch sampling procedure was used until all branches were measured. In order to reach most branches on the standing trees extension ladders and a swing system (see Figure 4) employing a boatswain's chair were used.

Figure 3. Photo showing fir branch sampling in the field.

Figure 4. Photo of 'swing system' (boatswain's chair) being used on a spruce.

When initially cutting the branches a series of four extension ladders (each 3.5 m long) were used. The ladders were placed on one another as the branch sampling progressed up the bole. Some trees, however, were too tall to have all their branches sampled by use of the ladders alone. Therefore, a researcher would climb up from the top of the ladders (15 meters high) onto the trees branches and up the remaining unsampled bole. Upon reaching a point on the bole where the diameter was approximately 10 cm, the researcher would securely strap a steel plate to the stem. Onto this plate was attached a pulley through which a long rope was passed. Attached to one end of this rope was a boatswain's chair or swing. Thus a researcher could sit in this chair and be pulled up the tree to sample the remaining branches. Those branches above the steel plate and hence out of reach of the swing were sampled after the tree was felled. To minimize destruction of these remaining branches in the fall, some trees were lowered slowly while being felled by use of the same steel plate and rope.

The intensive sampling method for branches described above was followed rather closely for subalpine fir with only a few exceptions. Because of the greater number of branches every twentieth branch instead of every tenth was sampled. The azimuth position was not recorded for fir or aspen branches.

For aspen all branches were denuded at once, but bagged by three meter intervals. After defoliation, wood and bark sampling was done. Every tenth branch was divided into twigs and main branch and appropriate samples taken from both. All dead branches on aspen, fir and spruce were cut, weighed and piled. After all dead branches had been collected a suitable sample was bagged and brought back to the lab for green to dry weight determination.

For extensive sampling of branches of spruce, aspen, and fir every tenth or twentieth branch was cut off a number of trees and D.O.B. (Diameter Outside Bark), D.I.B. (Diameter Inside Bark), total green weight and length were recorded.

At the lab the oven-dry weights of the various bagged components from intensively sampled trees were recorded. Dry weights were obtained by storing the bags at a temperature of approximately 100 degrees centigrade for several days to several weeks depending on the size and nature of the components. Oven dry weight was reached when successive weighing of the components revealed no further drop in weight.

The samples were then carefully weighed and recorded. By knowing the sampling percentage a suitable blow-up factor was applied to each category's sample components to arrive at total wood and bark dry weights for each category (main branch, leafy twigs, etc.). Total wood dry weight and bark dry weight were then obtained by personally written computer programs for each intensive branch. After regression analysis (using independent variables such as D.O.B., D.I.B., total length and total green weight) was completed it was found that for all three tree species green weight of the branch best predicted the total drv wood or dry bark weight for the branch. These equations (six in all) were then used on the green weights recorded for each sample branch on the extensive trees. This figure was then multiplied by a suitable blow-up to obtain total branch wood and total branch bark biomass for each tree. These total tree figures were then used in a regression analysis to determine which independent factor was the best predictor of total tree branch wood or bark biomass.

Production estimates of branches according to Whittaker (1965) are difficult because of a "very wide range of branch vigor ...." Branch production was calculated in two ways. The first method used is the mean annual increment (MAI) method or as it's referred to by Whittaker and Marks (1975), the relative production rate.

To obtain the relative branch wood and relative branch bark production the total branch wood and total branch bark biomass was divided by the total age of the tree. In the case of fir and aspen where the dead branches were weighed these were added to the biomasses and then divided by the tree's age. The total age of the trees was determined by aging the stump (one foot above the ground) and then adding on the estimate of years to reach stump height. The second method involves calculating the average of the last ten years' production by measurement of the radial increment on slabs cut along the bole. By use of the following formula (Whittaker 1965):

$$\frac{\Delta B}{B} = \Delta K \; (S/S)$$

where ΔB and B are branch production and biomass, ΔS and S are bole production and biomass, and K is the ratio of their relative growth rates; an estimate of branch production is possible. Calculation of K using MAI estimates produced consistent K values of 1.0 for spruce and fir with aspen showing considerable variance (from .8 to 2.0). Therefore in calculating aspen production individual tree values of K were used whereas an average value of 1.0 was used for fir and spruce.

Bole

The bole is defined as the main part of the tree above the stump and up to the point where it loses its character. For intensive and extensive trees there was no difference in bole sampling. There were, however, differences between species in sampling.

The spruce trees were sampled on an area that was to be clearcut and sold, therefore dissection of the bole could only be done in sixteen foot sections on the sold timber. Since transport or weighing of the entire bole was impossible, four to six inch wide slabs were taken at every sixteen foot interval, weighed green, then D.O.B., D.I.B., radial increments and ages were taken. The slabs were then brought back to the laboratory. At the laboratory the slabs were volumized by submersion and displacement of water. The slabs were submersed with bark on and then without the bark to arrive at separate wood and bark volume figures. The slab wood and bark were then oven dried for several weeks. It must be noted that due to the flaky nature of spruce bark some bark was lost in transport.

Back at the lab, therefore, a piece of clear plastic with a grid on it was placed along the outside of each slab. Lost bark was easily seen because of the brighter color underneath. From the grid an estimate of square inches of bark lost were thus calculated. After some experimenting the average weight and volume of a number of square inch bark chips was determined. Thus estimates of lost weight and volume of bark for each slab were calculated. From total dry weight and volume, specific gravity of the component was determined by using the formula:

$$\text{specific gravity} = \frac{\text{oven dry weight}}{\text{weight of water displaced}} .$$

Because of a lack of equipment, a scale procedure described by Collett (1963) could not be used.

The volume of each log was calculated by using the green D.O.B. and D.I.B.s of each slab. Volumes were calculated on an individual basis by use of Smalian's formula (Avery 1967). These volumes were then multiplied by the average specific gravities found for the slabs at either end of the particular log in question. By adding all the logs for each tree, estimates of bole biomasses were generated. For aspen and fir, four to six inch wide slabs were taken at the base, midpoint and tip of the bole. These slabs were taken back to the lab. Their D.O.B., D.I.B., radial increments, ages, and green weights were measured. They were then stripped into wood and bark and dried. The remaining boles were cut into small sections and completely weighed green in the field. The slabs green to dry weight and wood to bark ratios were used to calculate the total bole dry wood and bark biomass.

The MAI production method for the bole consists of taking total bole wood and total bole bark biomass and dividing by the total estimated tree age. For the yearly average of the last ten years production (PAI) the last ten year radial increments on the base and mid-slabs were measured, divided by ten (to obtain the yearly average of the last ten years) and expressed as a percent of total volume measurement. This percentage was multiplied times the total wood or total bark biomass to arrive at a production estimate.

Stump and roots

The stump and roots are those parts of the tree under one foot above the ground. The roots are by far the hardest part of the tree to estimate. Leith (1968) said that obtaining data for roots may require three or five times more labor than all other tree parts combined. On very large trees this can be an understatement. There are various methods to arrive at root biomass, none satisfying, none complete.

Complete root excavation by picks and shovels (or 'hand methodology' according to Gifford 1964) can be used. Other complete excavations have used water pressure (Stout 1956, Singer et al. 1965) and air pressure (Weir 1966). There is also a subtler approach, that of using dynamite and a power wench (Whittaker and Woodwell 1968). Sampling root systems by soil cores (Bray et al. 1959, Ovington et al. 1963) and soil blocks or pits (Leith 1968, Jenik 1971) are other ways at arriving at root biomass estimates.

Westlake (1968) thought that excavation of roots overestimates biomass and core sampling underestimates. Because of a lack of water the hydraulic approach was not possible so for fir and spruce the 'hand method' (spoons, picks and shovels) was used. Some root data on spruce and fir were supplied by Dr. T. W. Daniel (1977). A large spruce and fir root system were excavated along with some small firs. Roots were followed out from the stump until they were approximately one centimeter in diameter. They were then cut, weighed and piled for later sampling (see Figure 5).

A sample of roots and stump were weighed green and taken back to the lab for dry weight determination. Since aspen is clonal in nature (Day 144, Gifford 1964, Barnes 1966), three randomly placed cubic

Figure 5. Photo of partially excavated large fir stump and root system.

meter pits were excavated in each of the four separate clones. The d.b.h., age and distance from the pit center of the four nearest trees were measured. Solar radiation at each pit center was also measured. All roots down to approximately five millimeters in diameter were collected and bagged. The roots were brought back to the lab, dried and weighed. Thus total pit root biomass was obtained.

As for estimates of root production, none were attempted. In excavating these root systems, it becomes clear that there is a very large proportion of roots that are not recovered (rootlets, root hairs, etc.), thus using the ratios similar to the type used in estimating branch production would be useless. Newbould (1968) also stated that there are three problems with root production estimates. One is the turnover of small roots and root hairs. Second, is the disturbance of the root environment (i.e., using pot grown plants or glass interfaces). Thirdly is the variability among root systems. Because of these reasons root production was not estimated.

Reproduction

Because there were a large number of trees below breast height (1.38 meters), nine of these sub-d.b.h. trees of each species were sampled. The total wood and bark biomass (bole and branch together) were dried and measured. Basal diameter was measured and regressions were forced through zero.

Stand Biomass Estimation

To arrive at a stand biomass or production estimate, the d.b.h. of every tree on the study or target plots were taken. The resulting stand tables were then used in conjunction with predictive equations to estimate stand biomass and production. For instance, the diameters of all spruce trees on a certain plot were recorded. To arrive at an estimate for the spruce bole wood stand biomass, the spruce bole wood biomass equation (which like all other equations generated uses d.b.h. as the independent variable) is applied to each spruce tree's d.b.h. in the stand. All bole wood values generated for the spruce trees are then summed to arrive at a total spruce bole wood stand biomass estimate.

RESULTS

Thirty-two engelmann spruce trees were used for biomass determination. The results show that diameter at breast height (d.b.h.) and its transformations were the best independent variables used in the prediction of spruce biomass. As seen in Table 2 and Figures 6A, 7A-B, d.b.h.^{2} was the best predictor of bole wood, branch bark, and branch wood biomass. D.b.h. untransformed was however, the best predictor of spruce bole bark biomass (Table 2, Figure 6B). The use of combinations of other independent variables (i.e., d.b.h. and height) were avoided because of complications caused by multicolinearity (Jensen 1977). Twenty fir trees were used for biomass determination. Depending on the data available, not all trees were used in each category. For bole wood, bole bark, branch wood and branch bark biomass, d.b.h.^{2} was the best predictor (see Table 2 and Figures 8A-B, 9A-B). For aspen twenty trees were used for biomass calculations. Bole wood and bole bark biomass were correlated to d.b.h.^{2}. Branch wood biomass was best predicted by d.b.h.^{3} while branch bark biomass was best correlated to a log-log transformation with d.b.h. as the independent variable (Table 2, Figures 10A-B, 11A-B). For any data in this report, please refer to the Appendix.

For engelmann spruce, bole wood MAI is the best correlated with d.b.h. Bole bark MAI is best predicted by a log-log transformation with d.b.h. as the independent variable (Table 3, Figures 12A-B). The branchwood and bark MAI were best predicted by using a linear

Table 2. A compilation of aspen, fir, and spruce biomass equations.

Dependent variable (kg)	Coefficients** A	Coefficients** B	Independent variable (cm)	R^2	Standard error of the estimate
Spruce bole wood	-65.96	.338	dbh^2	.96	36.141
Spruce bole bark	-18.17	1.501	dbh	.89	9.352
Spruce branch wood	1.48	.031	dbh^2	.89	16.260
Spruce branch bark	3.25	.023	dbh^2	.88	12.050
Small spruce wood and bark*	0	9.381	basal $dia.^3$	.99	162.387
Fir bole wood	-12.25	.190	dbh^2	.98	34.034
Fir bole bark	-3.32	.035	dbh^2	.94	11.091
Fir branch wood	1.95	.029	dbh^2	.95	8.018
Fir branch bark	1.46	.022	dbh^2	.95	6.027
Small fir wood and bark*	0	11.241	basal $dia.^3$	.99	157.909
Aspen bole wood	3.06	.179	dbh^2	.97	19.400
Aspen bole bark	-3.62	.061	dbh^2	.90	13.141
Aspen branch wood	1.67	.0007	dbh^3	.93	5.252
Aspen branch bark***	-2.01	2.102	$\log_{10}$ dbh	.91	.216
Small aspen wood and bark*	0	9.340	basal $dia.^3$	.98	237.819
Fir and spruce stump and roots	10.90	.00003	dbh^4	.99	8.168
Aspen pit roots+	A_0=2.028367E-03		A_4=1.705909E-05		
	A_1=-2.899394E-03		A_5=2.507922E-06		
	A_2=4.055455E-02		A_6=-5.233035E-08		
	A_3=-2.612289E-03				

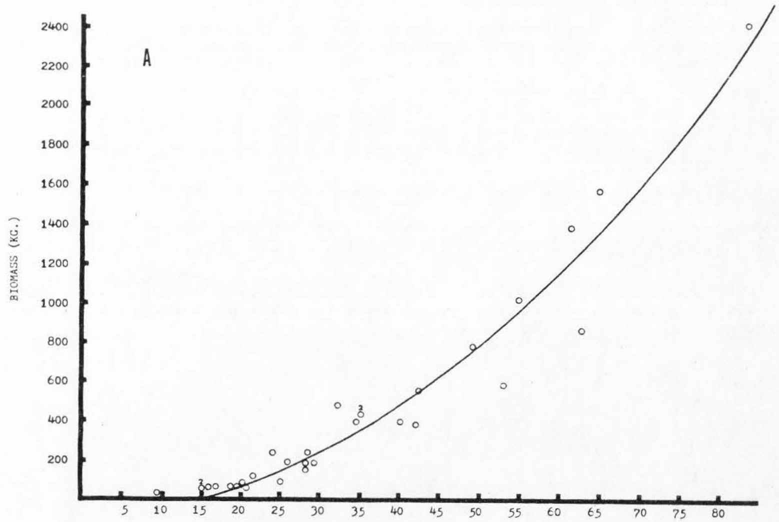
*expressed in grams **equation is in the form: Y=A+BX.

*** means $\log_{10}$ (dependent variable) + no regression was used, instead of the form: $Y = A_0+A_1X+A_2X^2+ \ldots A_6X^6$ was applied to a handfit line, where X is d.b.h. Of the four nearest trees to pit center divided by their distance, E represents in polynomials base 10.

Table 3. A compilation of aspen, fir, and spruce MAI equations.

Dependent variable (kg/ha/yr)	Coefficients** A	Coefficients** B	Independent variable (cm)	R^2	Standard error of the estimate
Spruce bole wood	-2.02	.126	dbh	.91	.706
Spruce bole bark***	-3.35	1.681	$\log_{10}$ dbh	.72	.235
Spruce branch wood	-.14	.012	dbh	.77	.115
Spruce branch bark	-.07	.008	dbh	.74	.008
Fir bole wood	-.005	.002	dbh^2	.99	.222
Fir bole bark	-.019	.0003	dbh^2	.97	.067
Fir branch wood	.027	.0004	dbh^2	.95	.130
Fir branch bark	.022	.0003	dbh^2	.95	.098
Aspen bole wood+	A_0=.850789		A_4=7.495280E-05		
	A_1=-.250184		A_5=-1.084708E-06		
	A_2=3.820858E-02		A_6=5.261417E-09		
	A_3=-2.350578E-03				
Aspen bole bark+	A_0=1.9850		A_4=4.25095E-05		
	A_1= -.4548866		A_5=-5.334458E-07		
	A_2=4.04851E-02		A_6=2.4855762E-09		
	A_3=-1.74198E-03				
Aspen branch wood+	A_0=.236476		A_4=3.4980E-05		
	A_1=-9.44815E-02		A_5=-5.9986E-07		
	A_2=1.43314E-02		A_6=3.84929E-09		
	A_3=-9.7838E-04				
Aspen branch bark+	A_0=.10528		A_4=1.7075E-05		
	A_1=-4.0010E-02		A_5=-3.34229E-07		
	A_2=5.9225E-03		A_6=2.4190E-09		
	A_3=-4.2161E-04				

equation is in the form: Y = A+BX. * means $\log_{10}$(depend. var.)
+ no regression was used, instead a polynomial of the form: $Y = A_0+A_1X+A_2X^2+ \dots +A_6X^6$ was applied to a hand-fit line, where X is dbh, E represents in polynomials base 10.



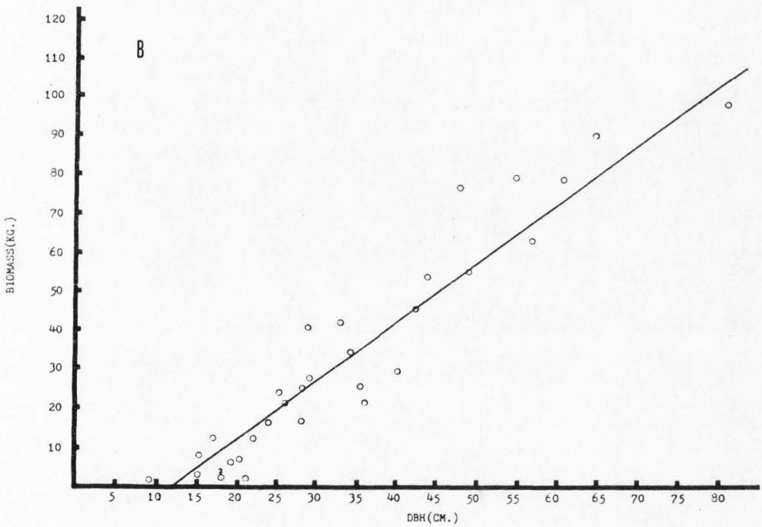


Figure 6. A-spruce bole wood biomass vs. dbh (regression line shown).
B-spruce bole bark biomass vs. dbh (regression line shown).

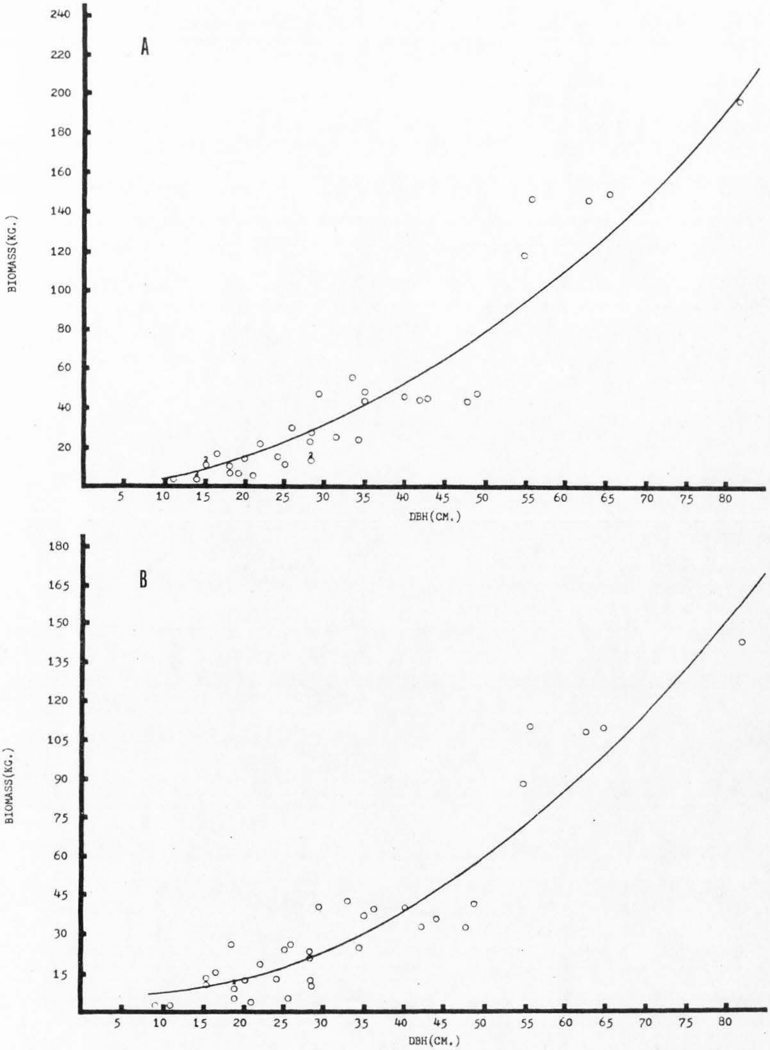


Figure 7. A-spruce branch wood biomass vs. dbh (regression line shown).
B-spruce branch bark biomass vs. dbh (regression line shown).

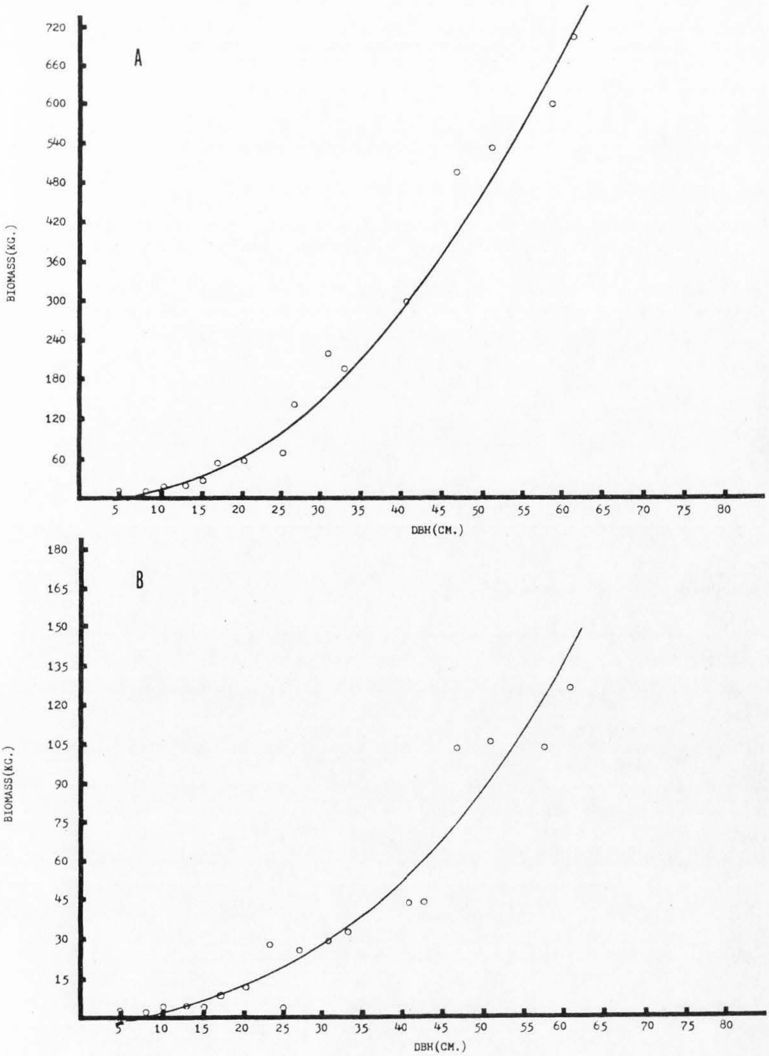


Figure 8. A-fir bole wood biomass vs. dbh (regression line shown).
B-fir bole bark biomass vs. dbh (regression line shown).

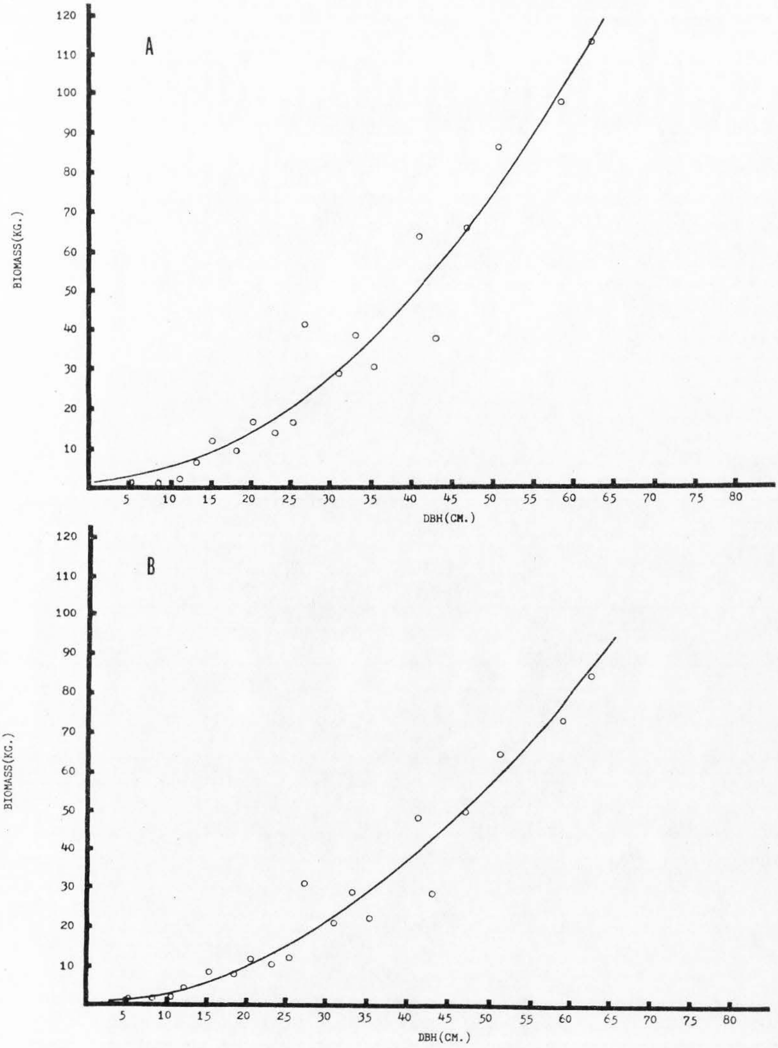


Figure 9. A-fir branch wood biomass vs. dbh (regression line shown).
B-fir branch bark biomass vs. dbh (regression line shown).

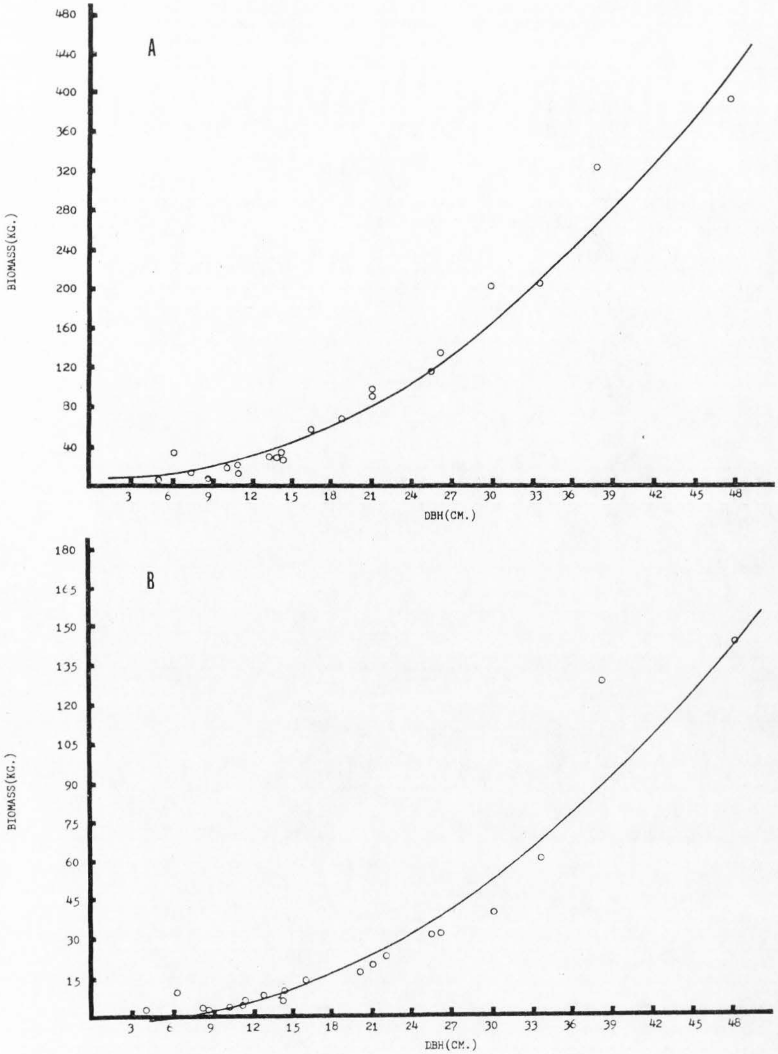


Figure 10. A-aspen bole wood biomass vs. dbh (regression line shown).
B-aspen bole bark biomass vs. dbh (regression line shown).

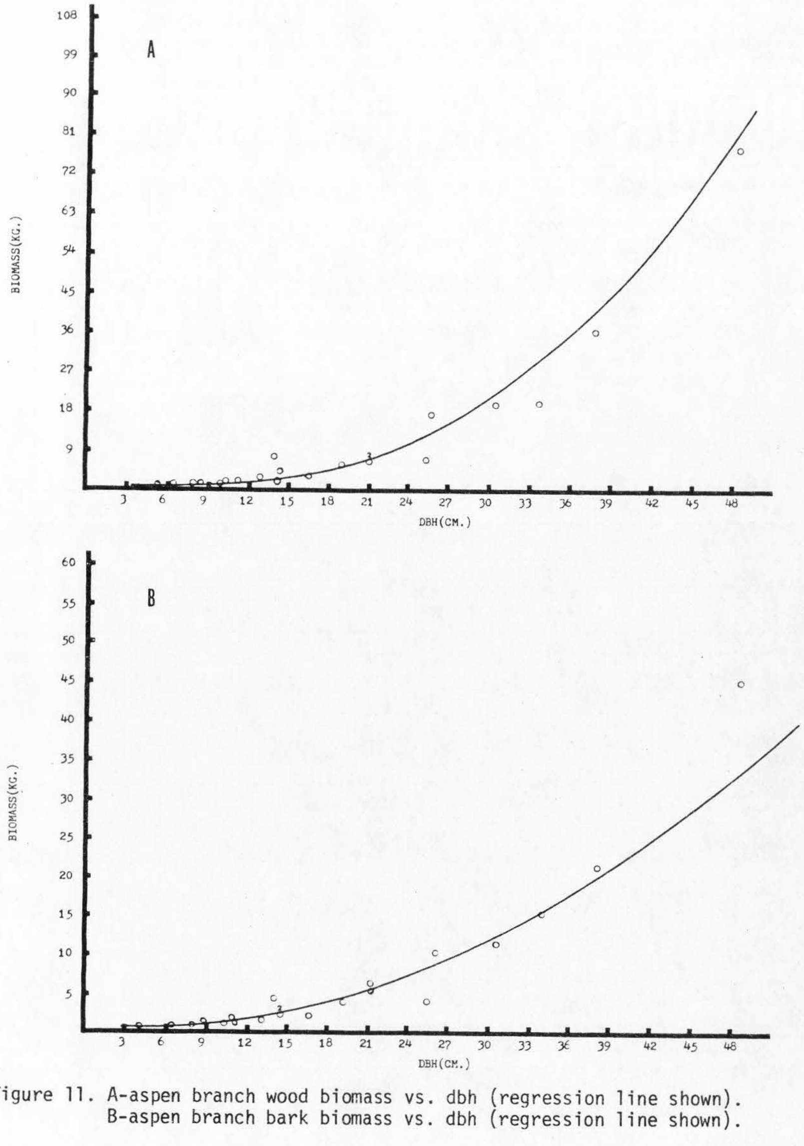


Figure 11. A-aspen branch wood biomass vs. dbh (regression line shown).
B-aspen branch bark biomass vs. dbh (regression line shown).

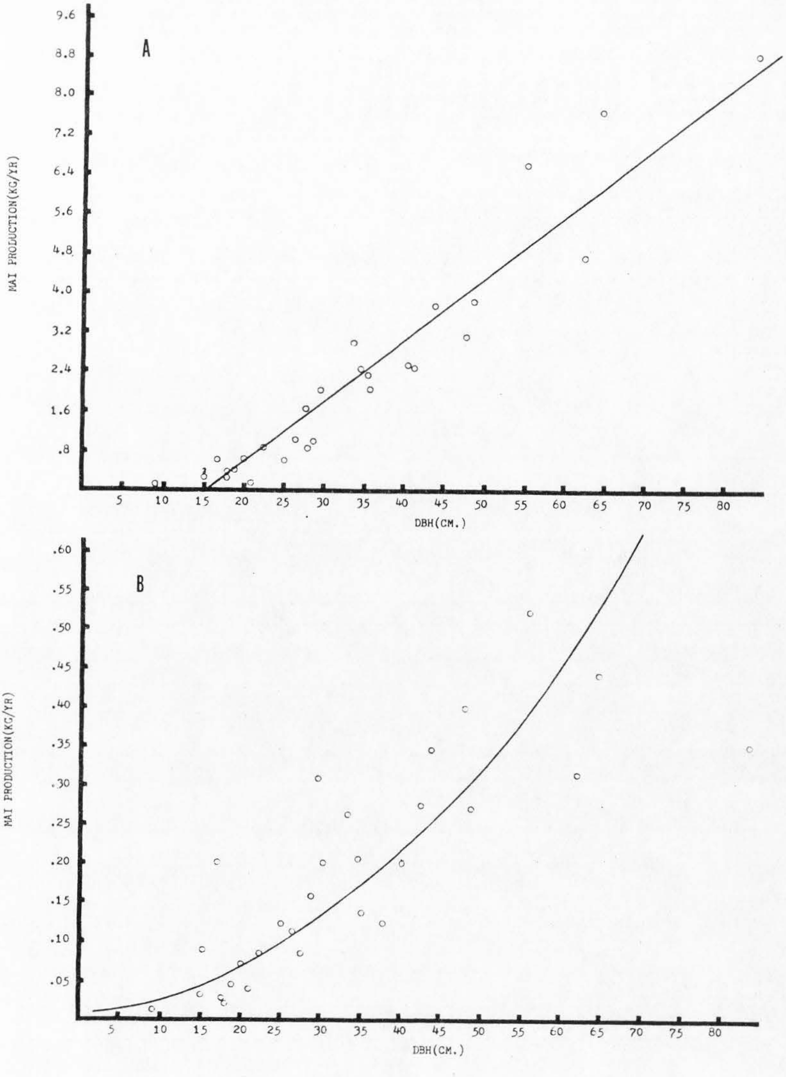


Figure 12. A-spruce bole wood MAI vs. dbh (regression line shown).
B-spruce bole bark MAI vs. dbh (regression line shown).

relationship with d.b.h. For the spruce PAI of bole wood, bole bark, branch wood and bark, polynomials were used (see Table 4, Figures 16A-B, 17A-B). The use of orthogonal polynomials in these particular instances was proposed by Jensen (1977). Orthogonal polynomials are being used to express relationships that because of a lack of points cannot be statistically made. For instance, some of the data at the upper range of diameters show a clear downward trend yet statistically fitting a line will not work.

Subalpine fir bole wood, bole bark, branch wood and branch bark MAI productions were all correlated to d.b.h.^{2} (see Table 3, Figures 14 A-B, 15A-B). The fir bole wood and bole bark PAI are best predicted by d.b.h. The fir branch wood and branch bark production are both best correlated with d.b.h. to the 0.3 power. For fir PAI equations and graphs see Table 4 and Figures 20A-B, 21A-B.

All aspen MAI and PAI equations were predicted by use of sixth degree polynomials with d.b.h. as the independent variable. The aspen MAI and PAI equations and graphs are in Table 4 and Figures 18A-B, 19A-B, 22A-B, and 23A-B. The reproduction biomass equations are shown in Table 2 and Figures 24A-B, 25A. As can be seen, basal diameter is the best predictor for all three species.

Spruce and fir stump and root biomasses seem to lie on the same curve and were thus combined. A total of seven fir and spruce were sampled from approximately three centimeters to 66 centimeters in d.b.h. As seen on Table 2 and Figure 25B, d.b.h. to the fourth power was the best predictor. Aspen pit root biomass was best correlated to the nearest four trees' average d.b.h.'s divided by the average of

Table 4. A compilation of aspen, fir, and spruce PAI equations.

Dependent variable (kg/ha/yr)	Coefficients A	Coefficients B	Independent variable (cm)	R^2	Standard error of the estimate
Fir bole wood	-.662	.119	dbh	.85	.951
Fir bole bark	-.152	.022	dbh	.77	.228
Fir branch wood	-1.078	.621	$dbh^{.3}$	.76	.184
Fir branch bark	-.811	.467	$dbh^{.3}$	.77	.139
Spruce bole wood+	A_0=-.661348		A_4=-7.186623E-06		
	A_1=.190436		A_5=3.770080E-08		
	A_2=-1.07090E-02		A_6=-3.081076E-11		
	A_3=4.731072E-04				
Spruce bole bark+	A_0=-.173633		A_4=-4.277425E-06		
	A_1=4.917060E-02		A_5=3.843235E-08		
	A_2=-4.683390E-03		A_6=-1.291043E-10		
	A_3=2.142561E-04				
Spruce branch wood+	A_0=-.225442		A_4=-3.940746E-06		
	A_1=5.586200E-02		A_5=3.4118398E-08		
	A_2=-4.61327E-03		A_6=-1.099880E-10		
	A_3=2.041183E-04				
Spruce branch bark+	A_0=-.548189		A_4=-7.524674E-06		
	A_1=.1317212		A_5=6.7226568E-08		
	A_2=-1.029008E-02		A_6=-2.300314E-10		
	A_3=3.996842E-04				
Aspen bole wood+	A_0=1.020154		A_4=-7.565248E-05		
	A_1=-.1871395		A_5=1.528225E-06		
	A_2=8.669985E-03		A_6=-1.042086E-08		
	A_3=1.183368E-03				

Table 4 Continued.

Dependent variable (kg/ha/yr)	Coefficients A	B	Independent variable (cm)	R^2	Standard error of the estimate
Aspen bole bark+	A_0=-.1770297		A_4=-5.197103E-05		
	A_1=.1262542		A_5=7.8388114E-07		
	A_2=-2.079236E-02		A_6=-4.470003E-09		
	A_3=1.573635E-03				
Aspen branch wood+	A_0=.553769		A_4=4.189605E-05		
	A_1=-.214220		A_5=-5.660386E-07		
	A_2=2.84584E-02		A_6=3.0278854E-09		
	A_3=-1.545147E-03				
Aspen branch bark+	A_0=.11651		A_4=-2.706616E-06		
	A_1=-3.35644E-02		A_5=7.870015E-08		
	A_2=2.998424E-03		A_6=-6.172107E-10		
	A_3=-3.094219E-05				

** equation is in the form: Y=A+BX. + no regression was used, instead a polynomial of the form: $Y=A_0+A_1X+A_2X^2+\ldots A_6X^6$ was applied to a hand-fit line, where X is dbh . E represents in polynomials base 10.

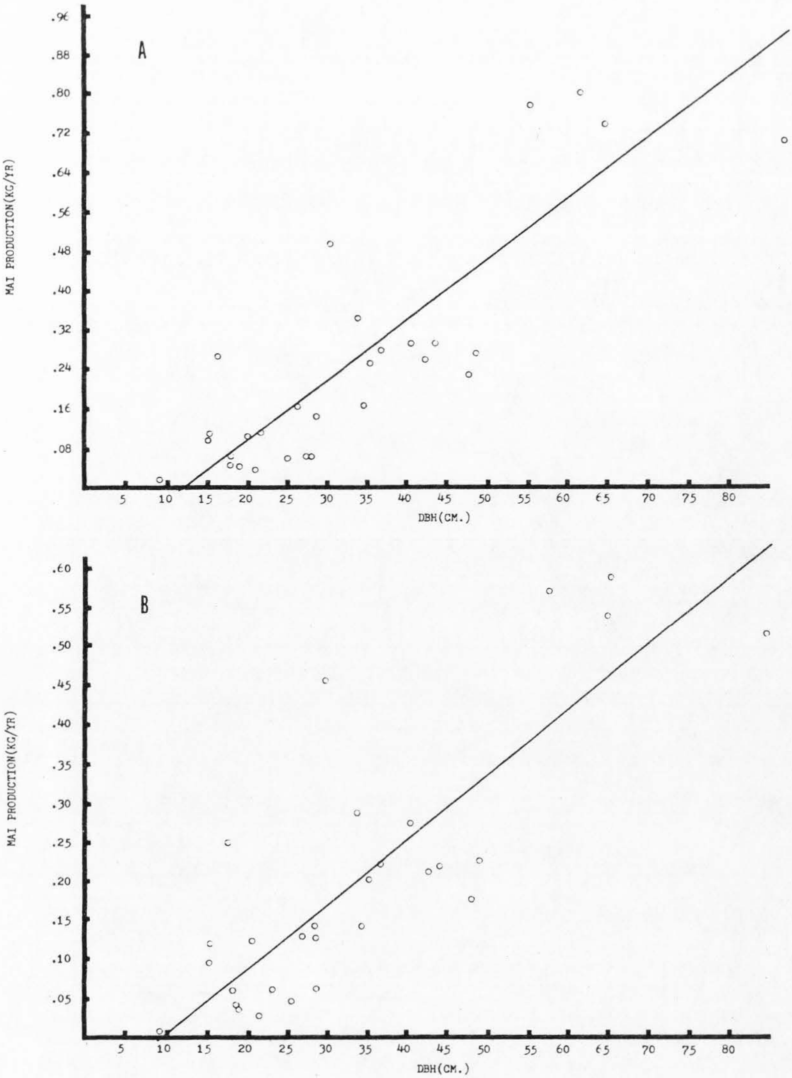


Figure 13. A-spruce branch wood MAI vs. dbh (regression line shown).
B-spruce branch bark MAI vs. dbh (regression line shown).

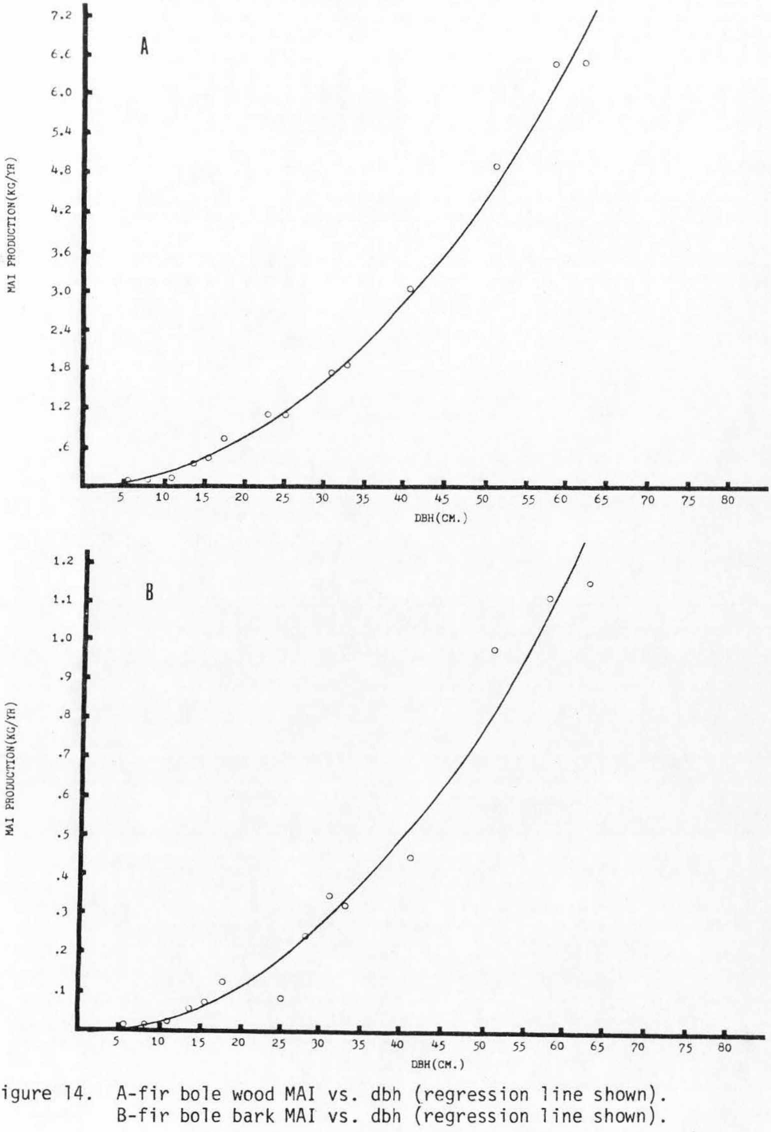


Figure 14. A-fir bole wood MAI vs. dbh (regression line shown).
B-fir bole bark MAI vs. dbh (regression line shown).

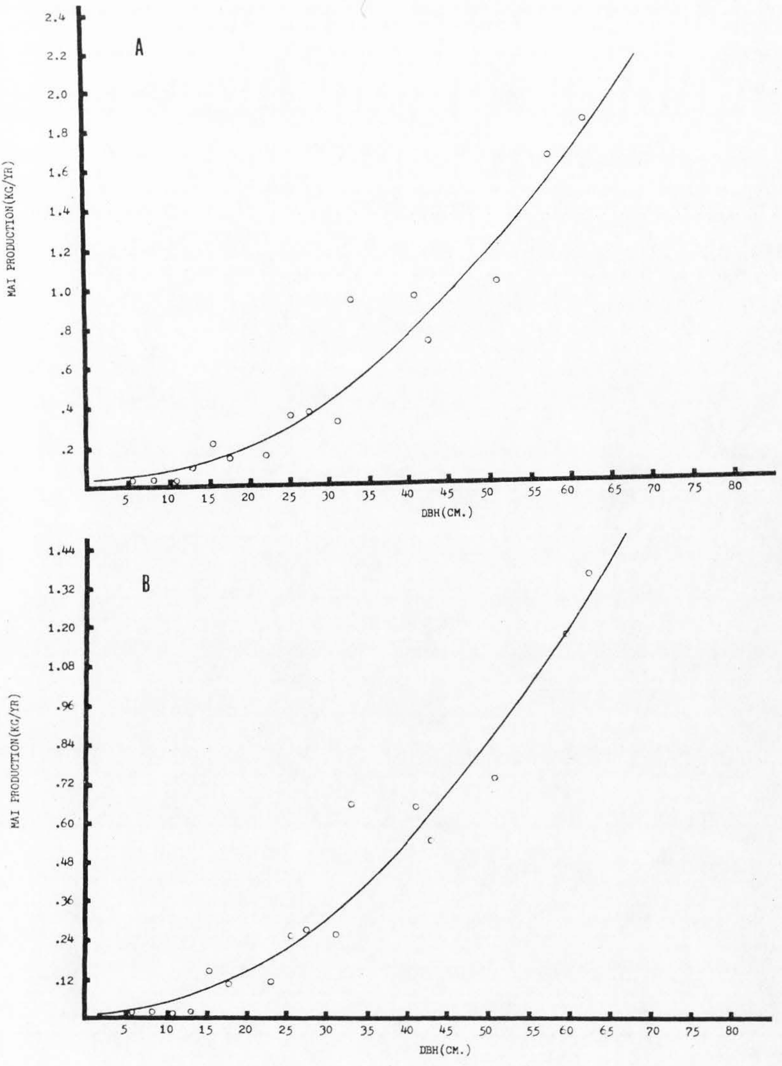


Figure 15. A-fir branch wood MAI vs. dbh (regression line shown).
B-fir branch bark MAI vs. dbh (regression line shown).

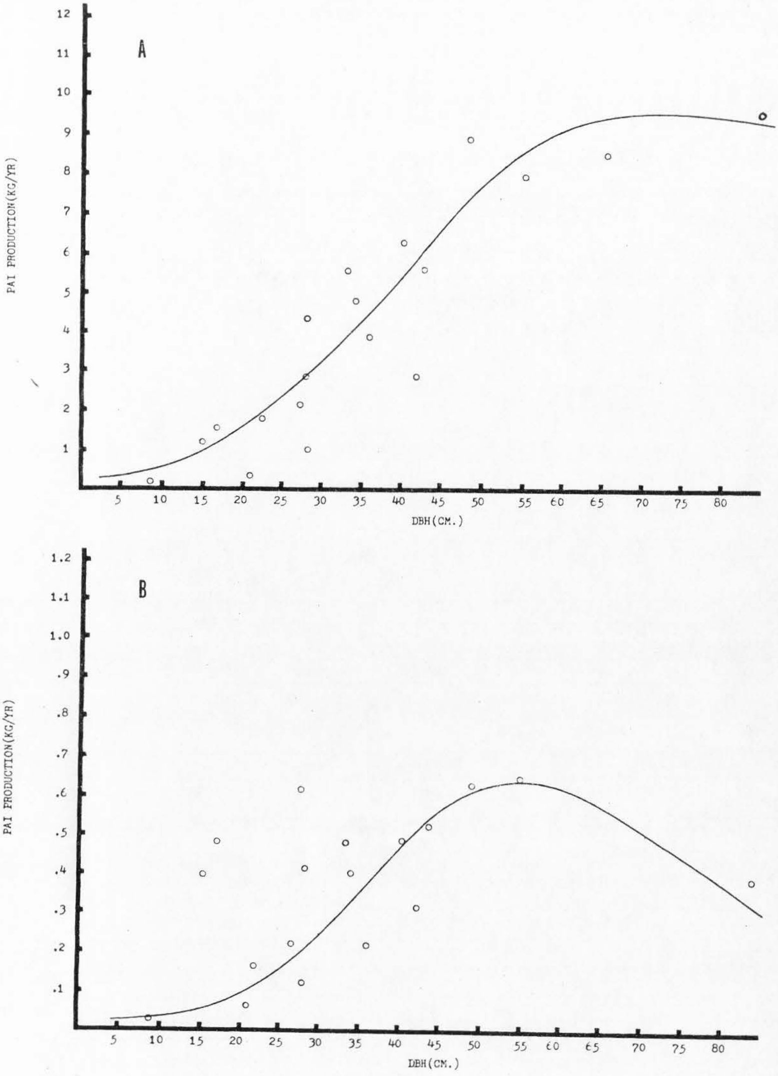


Figure 16. A-spruce bole wood PAI vs. dbh (hand-fit line shown).
B-spruce bole bark PAI vs. dbh (hand-fit line shown).

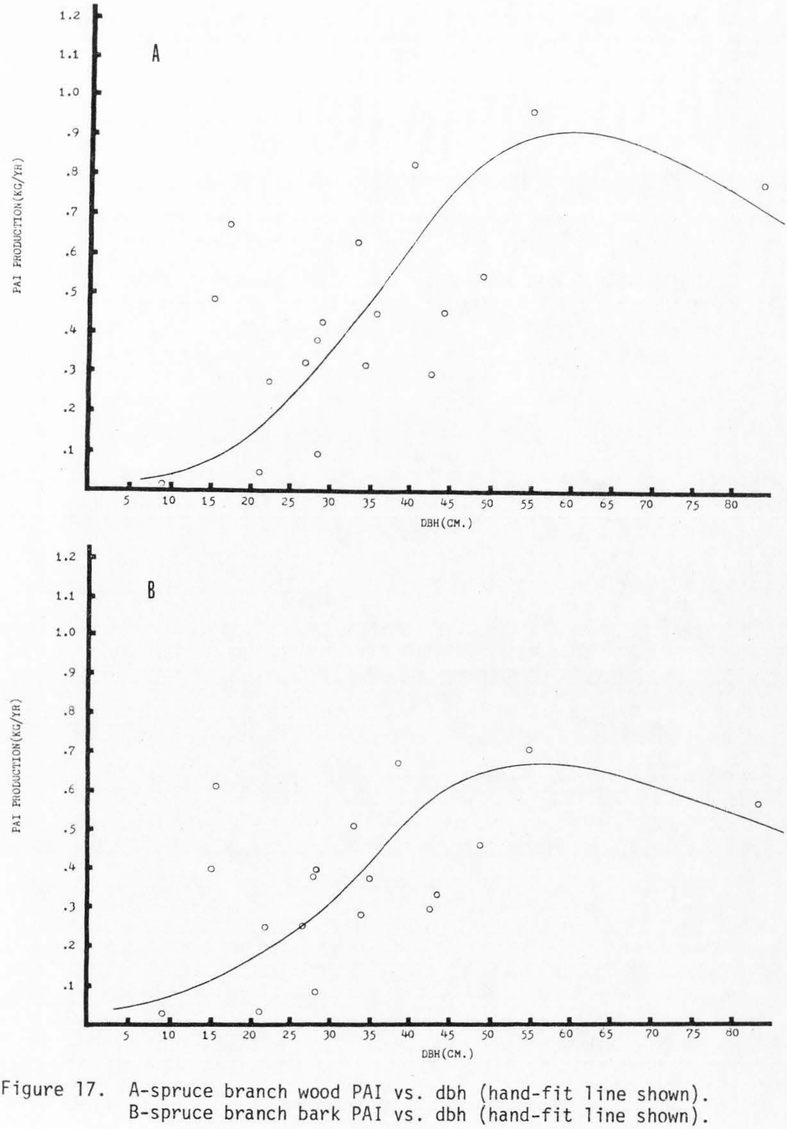


Figure 17. A-spruce branch wood PAI vs. dbh (hand-fit line shown).
B-spruce branch bark PAI vs. dbh (hand-fit line shown).

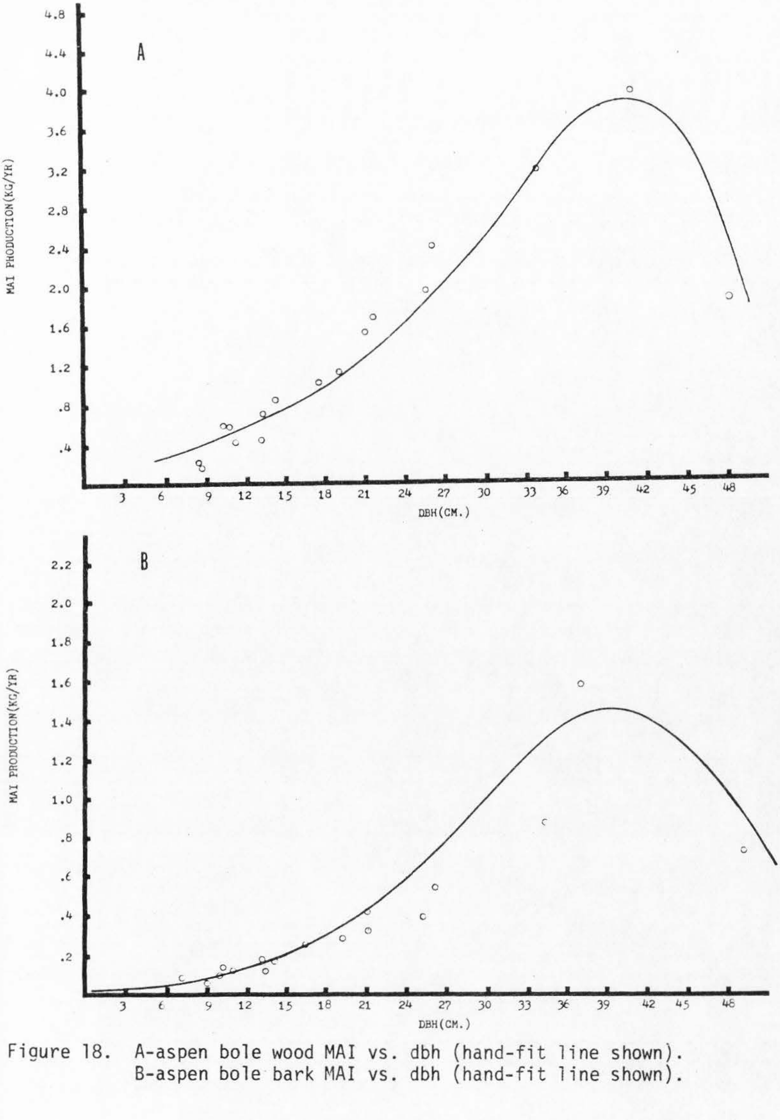


Figure 18. A-aspen bole wood MAI vs. dbh (hand-fit line shown).
B-aspen bole bark MAI vs. dbh (hand-fit line shown).

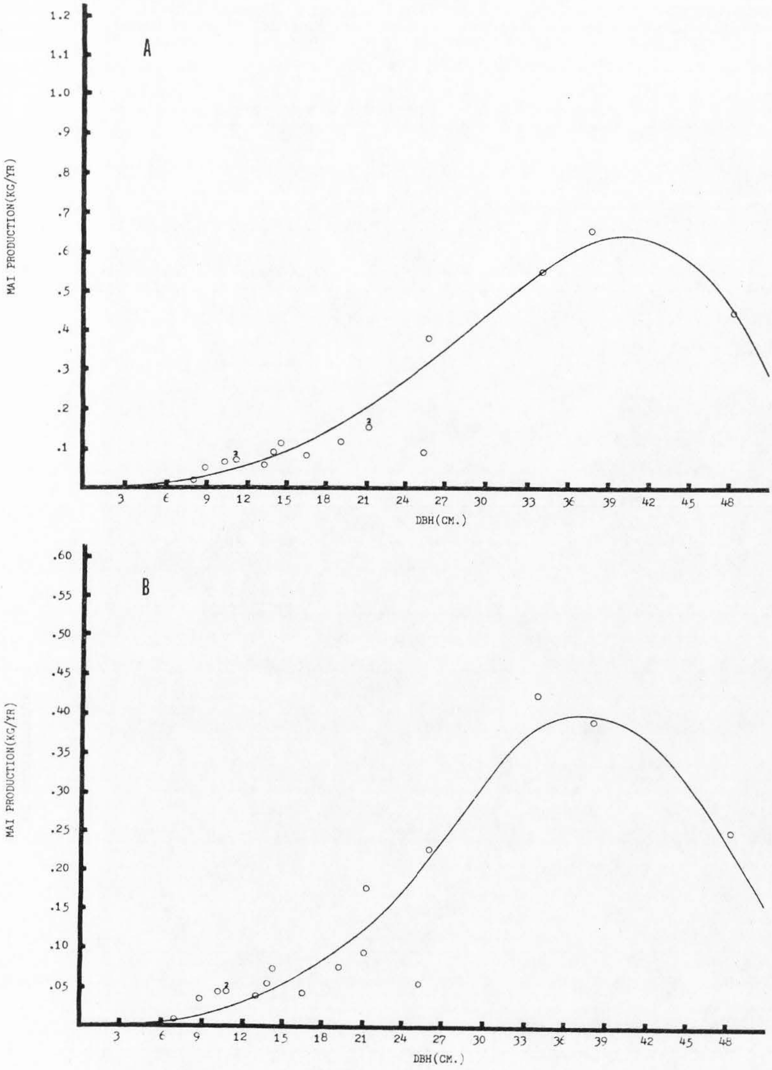
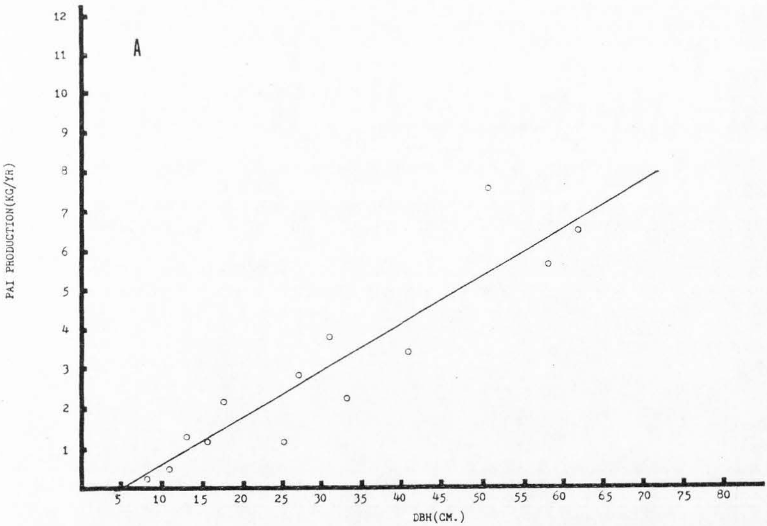


Figure 19. A-aspen branch wood MAI vs. dbh (hand-fit line shown).
B-aspen branch bark MAI vs. dbh (hand-fit line shown).



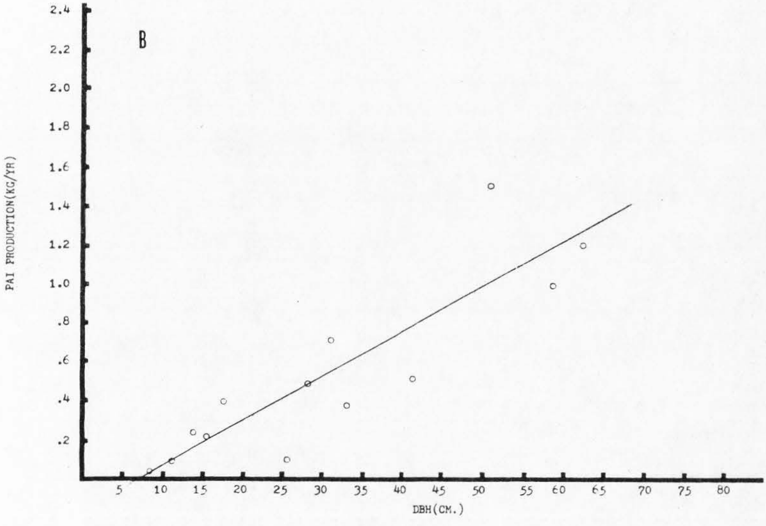


Figure 20. A-fir bole wood PAI vs. dbh (regression line shown).
B-fir bole bark PAI vs. dbh (regression line shown).

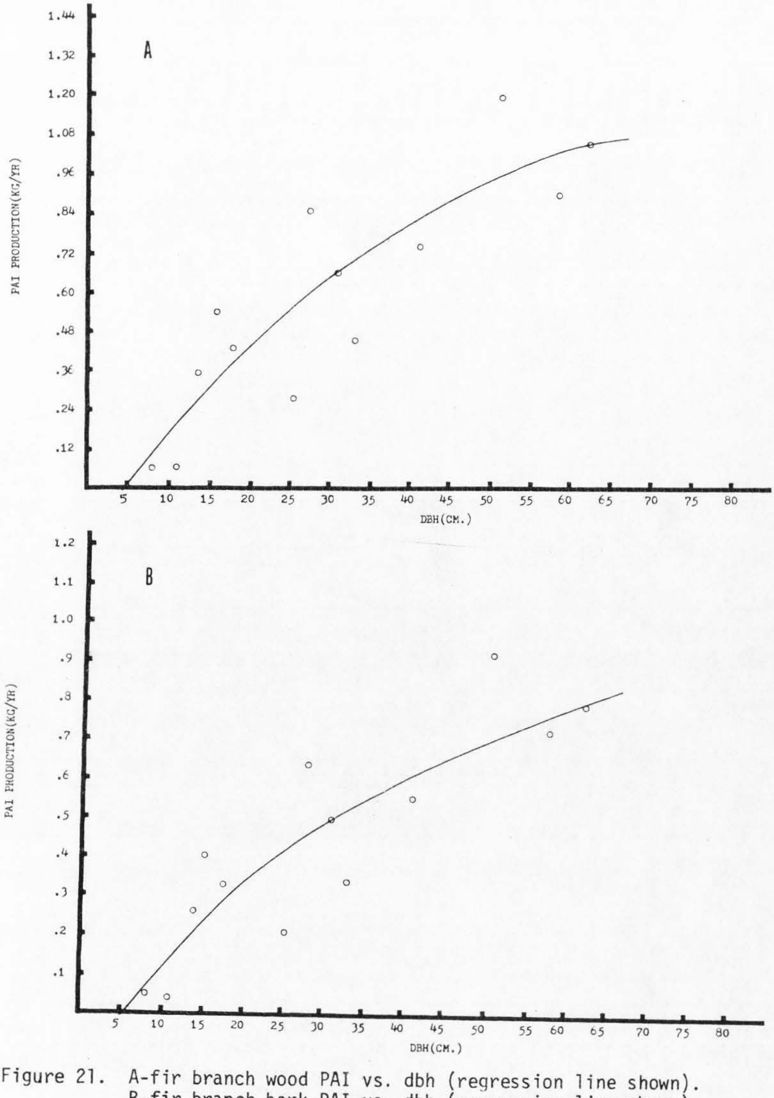


Figure 21. A-fir branch wood PAI vs. dbh (regression line shown).
B-fir branch bark PAI vs. dbh (regression line shown).

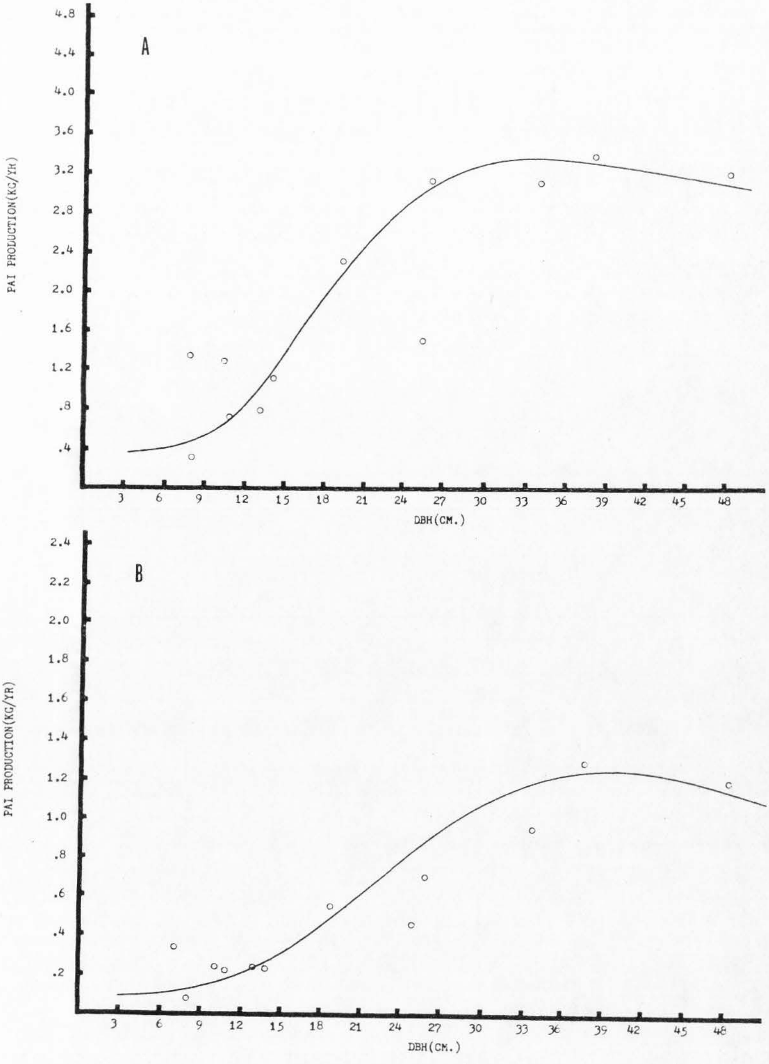


Figure 22. A-aspen bole wood PAI vs. dbh (hand-fit line shown).
B-aspen bole bark PAI vs. dbh (hand-fit line shown).

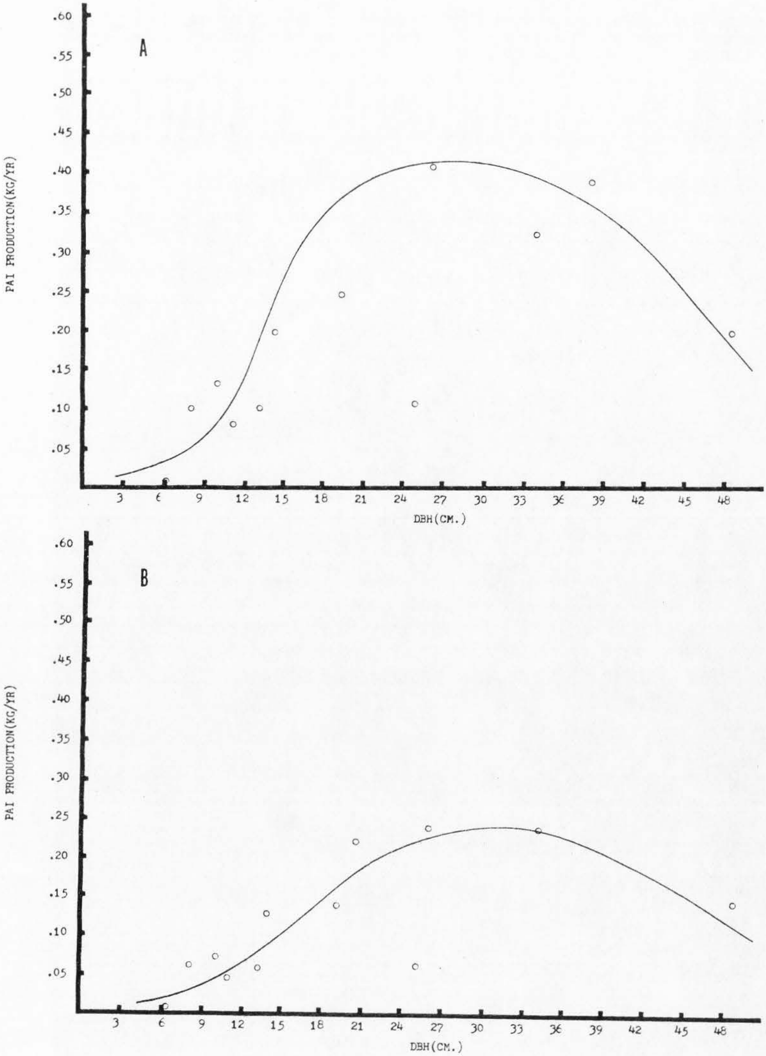


Figure 23. A-aspen branch wood PAI vs. dbh (hand-fit line shown).
B-aspen branch bark PAI vs. dbh (hand-fit line shown).

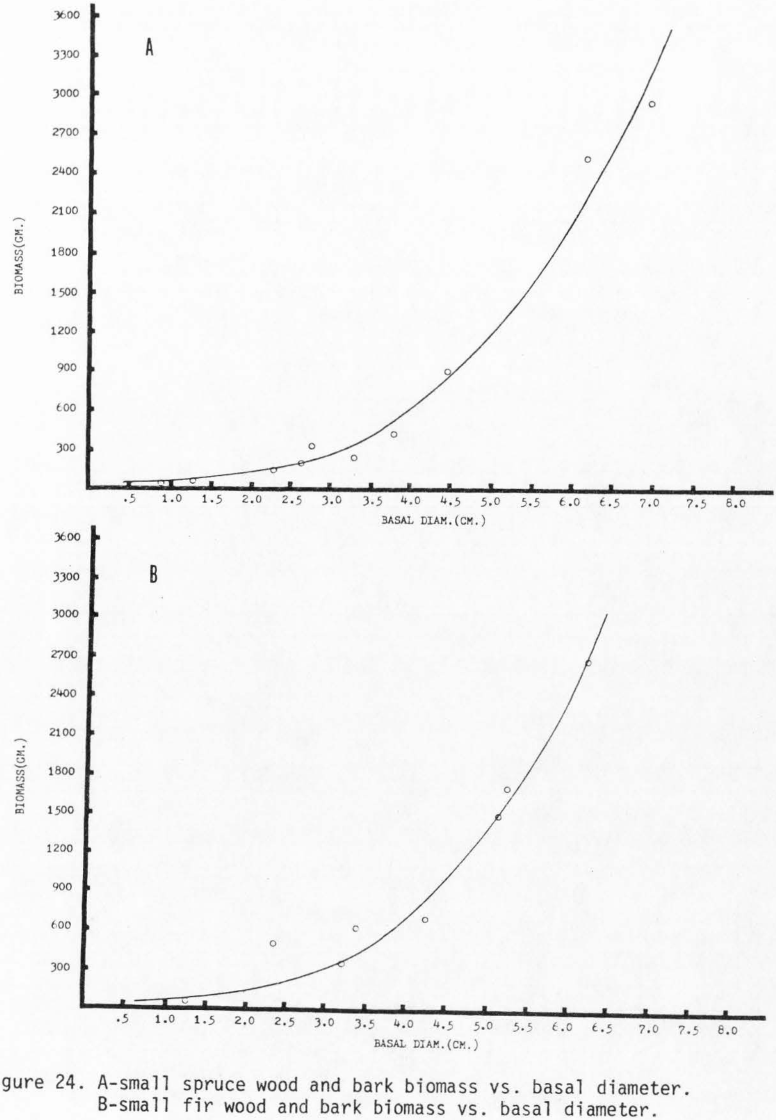


Figure 24. A-small spruce wood and bark biomass vs. basal diameter.
B-small fir wood and bark biomass vs. basal diameter.

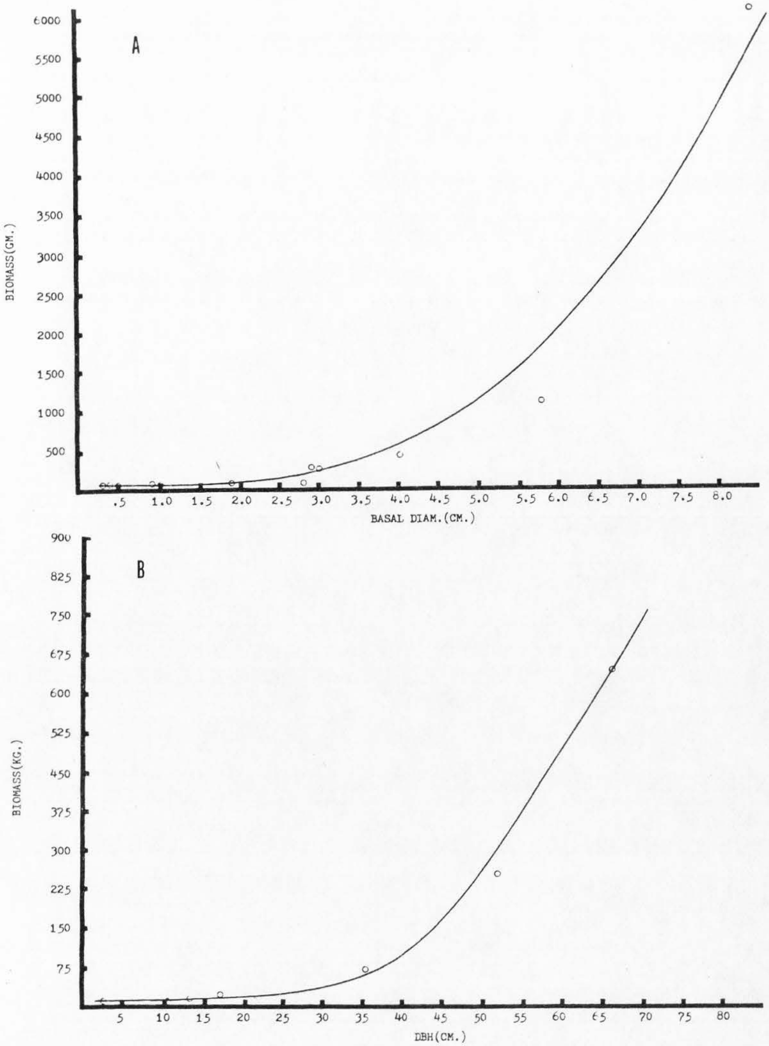


Figure 25. A-small aspen wood and bark biomass vs. basal diameter.
B-Fir and spruce stump and root biomass vs. dbh (regression line shown.

of their distance (in centimeters and meters) to pit center (Table 2, Figure 26A). Twelve pits in four clones (three random pits to a clone) were excavated. A polynomial was again used. When all of the above equations were applied to the stand tables of each plot, total plot biomasses and productions were generated. These are shown plotted against age (years since the plots were meadows) or successional time. Aspen pit biomass was obtained by using a computer program which placed hypothetical pit centers at one meter intervals in the center area (300 $meters^2$) of each 500 $meter^2$ plot. At each hypothetical pit the root pit biomass was estimated and then all pits were added together for total plot root biomass.

Total stand wood and bark (above and below-ground) biomass seems to increase exponentially through time (see Figure 26B). A breakdown by species for each stand can be seen in Figure 27A. Total MAI and PAI stand data both exhibit a bimodal distribution (Figure 27B), being high in early (aspen) stages, low in mid (fir) stages, and high again in mature (spruce) stages. A species breakdown of both production estimates are presented in Figures 28A-B.

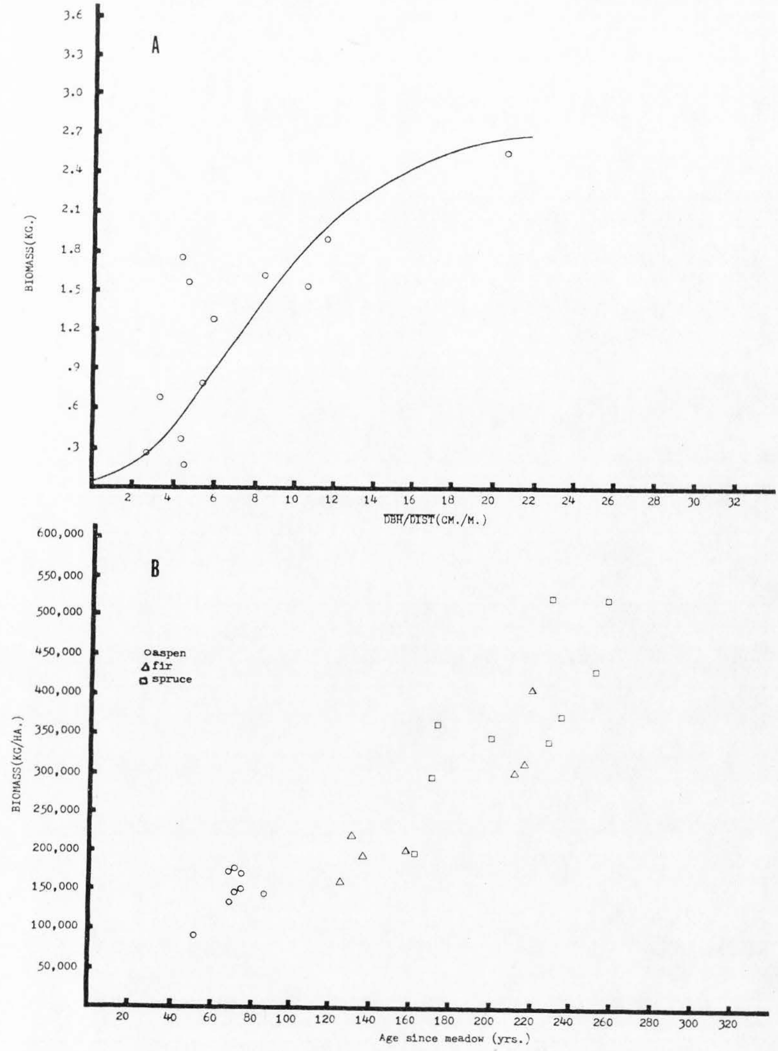


Figure 26. A-aspen root pit biomass vs. $\overline{\text{dbh/distance}}$ (handfit line).
B-total above and below ground wood and bark stand biomass vs. plot age since meadow.

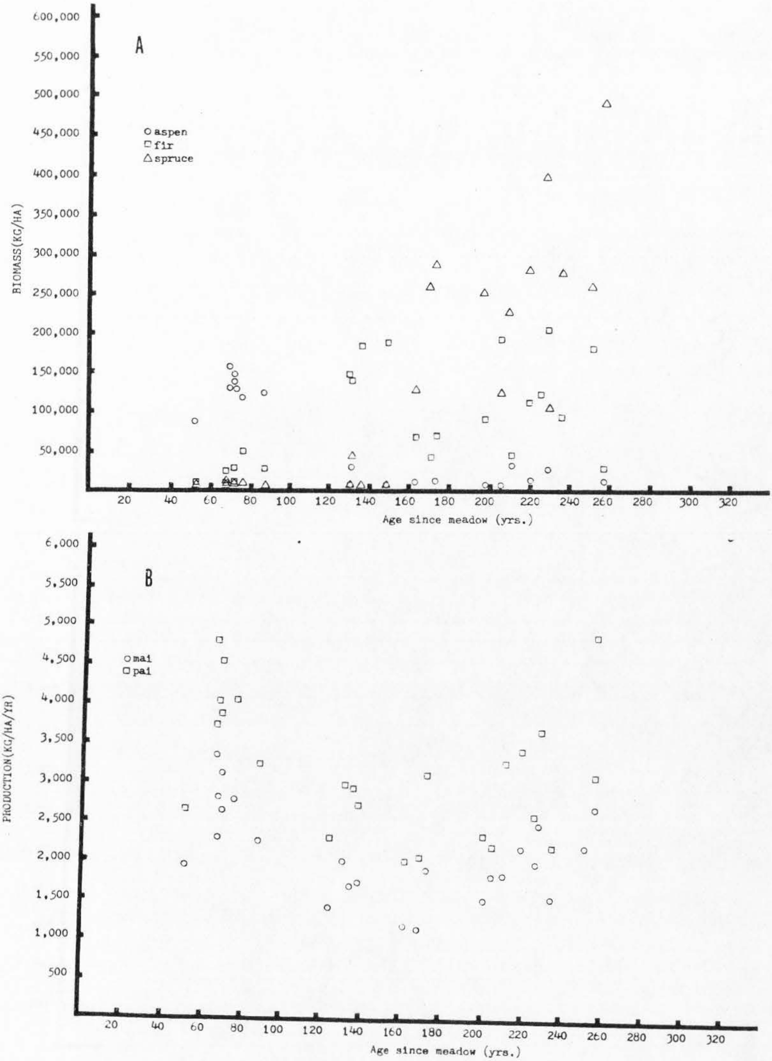


Figure 27. A-species breakdown of total stand biomass vs. plot age. B-total stand MAI and PAI vs. plot age.

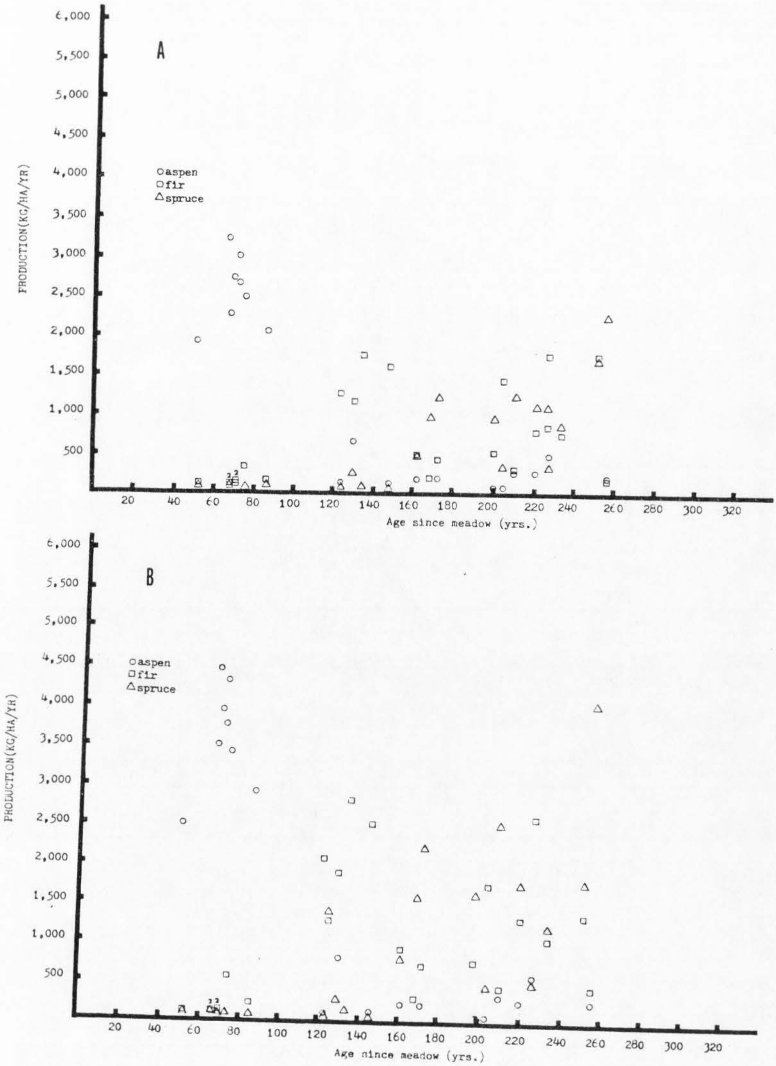


Figure 28. A-species breakdown of stand MAI vs. plot age.
B-species breakdown of stand PAI vs. plot age.

DISCUSSION

The specific gravities for the various spruce slabs were analyzed and varied from .284 to .477. The average specific gravity being about .38. These figures are higher than those found for spruce by Forrer (1969) but close to the .32 to .44 range found by Landis (1972). This study found the same increase in specific gravity with increase in height above the ground as both Landis (1972) and Forrer (1969) found. Bark specific gravity varied greatly in this study. Values were from .245 to .670. Some lower and higher values than these were found but were attributable to measurement errors. One large aspen tree was cut into slabs, volumized and weighed for specific gravity. The three wood specific gravity values were .36, .38 and .44 (increasing with height from the ground). This again corresponds closely to the approximate .31 to .44 range found by Landis (1977), the .325 to .421 range of Kennedy (1968), and the .34 to .45 range found by Schlaegel (1973). The aspen bole bark figures were .53, .56, and .48 (increasing with height from the ground). Schlaegel (1973) found aspen bark to range from .47 to .66.

Spruce bole wood biomass equations compare favorably with those of Landis and Mogren (1975) as shown in Figure 29. The differences which become pronounced in larger trees probably result from the lack of larger diameter trees used in the construction of regression equations and also the use of specific gravities and volume determinations which are less accurate than weighing the entire bole. It is interesting that spruce bole bark is more correlated with d.b.h. than its square.

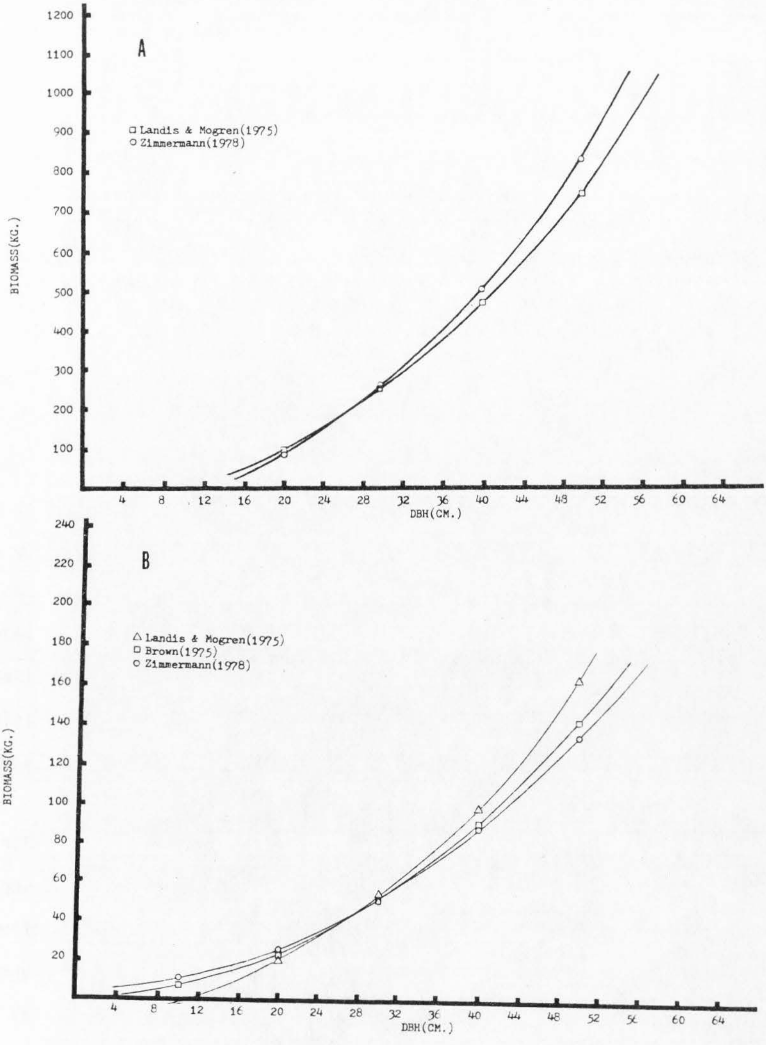


Figure 29. A-literature comparison of spruce bole wood values. B-literature comparison of spruce branch wood and bark values.

This is probably due to bark sloughing which is more common with spruce than fir or aspen. In fact, fir bole bark and aspen bole bark were correlated to d.b.h.^{2} and log-lon d.b.h. respectively thus demonstrating a faster rate of bark accumulation. Williams (1977) reports that spruce plots had significant (seven percent of total litterfall) amounts of spruce bark, more bark than any other successional stage thus verifying spruce bark loss. The spruce branch wood and branch bark equations also show the best correlation with d.b.h.^{2} The reason that d.b.h. and its square are the best independent variables for spruce and the other species has been explained biologically and mechanically by many researchers. Attiwill (1962, 1966) explains that the diameter along various points on the branches or the bole is related to the mechanical strength required to support the weight above. Attiwill goes on to say that the diameter is also related to the photosynthetic area above. This idea was taken a step farther by the pipe model theory (Shinozaki et al. 1964). The diameter or girth of a tree is, according to this theory, merely an accumulation of pipes, each pipe supporting a unit photosynthetic area. The relationship works best at the girth but changes at d.b.h. due to the accumulation of dead pipes that no longer possess a photosynthetic area.

A comparison of Landis and Mogren's spruce branch wood equation (1975) and this study's equation shows similar trends and values (see Figure 29B). On the same figure a study by Brown (1976) also shows similar values to those produced by our study. Figure 28B shows our study to be slightly higher in values for lower diameters, and lower in values for higher diameters when compared to Xrown, and to Landis and Mogren. With the error associated with all biomass regression equations, it can safely be said that all three studies have produced strikingly similar biomass figures. A comparison within, of our study's fir and spruce equations, show both species to have very similar relationships (compare values presented by our study in Figures 29B and 30A).

As stated above, fir and spruce biomass equations are very similar. Our study's fir branch wood and bark biomass predictions are also quite similar to those found by Brown (1976) as seen in Figure 30A. We are very close in values in the lower and mid diameter ranges, with some difference occurring in the higher diameters (Brown's equation predicts higher values).

Our study's aspen bole wood equation compares favorably with the corresponding equation of Landis (1972) as seen in Figure 30B. The equation Landis used incorporated d.b.h. inside the bark so a suitable conversion was used. From Figure 30B it can be seen that our values are higher than those of Landis in the lower diameter range but lower in the high diameters. Once again, the differences are surprisingly small. Landis had no bole bark equation so a comparison with our study's aspen bark equation was not possible.

Johnston and Bartos (1977) present equations for total above ground aspen biomass. By using their percent component graphs, values for above ground wood and bark were estimated. Comparing their two lines (for different stands) it can be seen that overall, our aspen biomass equations' predictions are close to theirs (see Figure 31). Peterson et al. (1970) present biomass equations for aspen clones near Calgary, Alberta. Their results also compared favorably to this study (Figure 31).

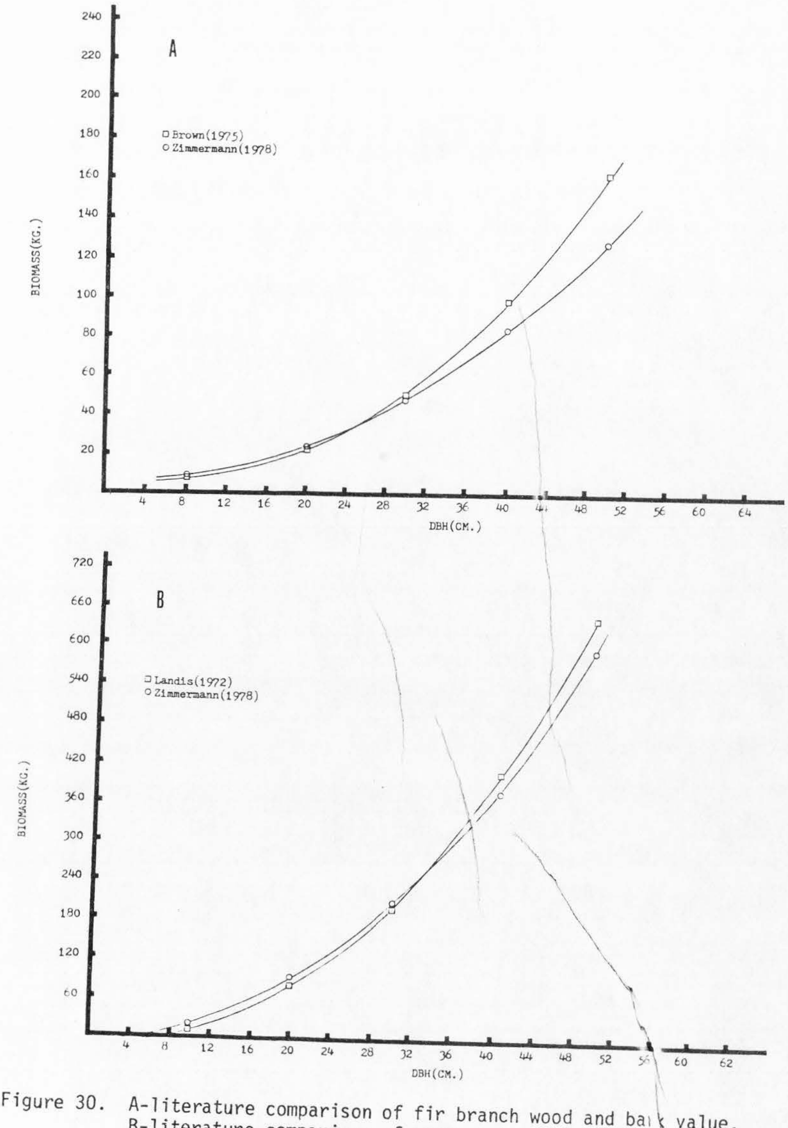


Figure 30. A-literature comparison of fir branch wood and bark value.
B-literature comparison of aspen bole wood values.

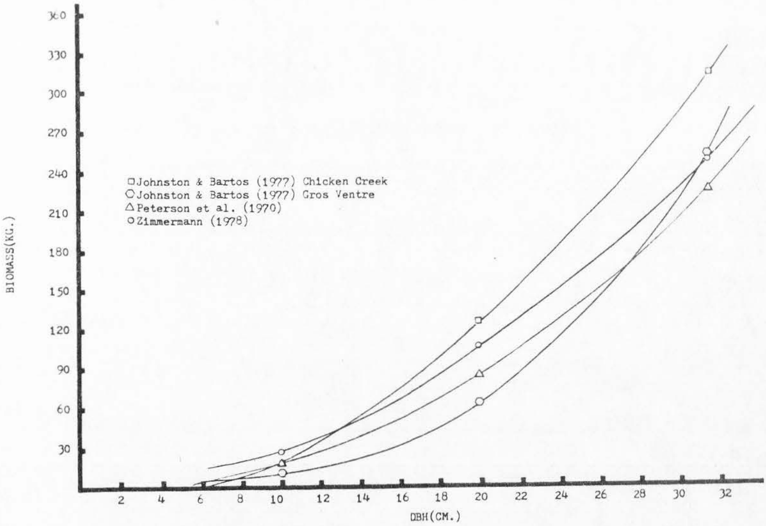


Figure 31. Literature comparison of aspen wood and bark above ground biomass vs. dbh.

Research on spruce and fir roots has been very limited. No biomass studies could be found, only qualitative research in terms of root distribution and length could be found. Kalela (1950) described the root distribution of pine and spruce stands in Germany. Nineteen spruce stands (ages 25-135 years) were studied. He found 87 percent of the roots in the top twenty centimeters of soil.

Kalela also calculates that roots over two millimeters form only 19 percent of the total roots in spruce. This information is based on linear centimeters of roots and not weight and therefore cannot be applied here.

While our project basically concerned itself with root biomass and did little with distribution it can be noted that in excavating our largest spruce tree we found a vast majority of the roots within the first .3 meters of soil. While excavating we would find "sinkers" however that would plunge straight down. A few such sinkers which were followed down to about 1.2 to 1.5 meters had little change in diameter. Under the large spruce stump, which lacked a taproot, roots were followed to approximately 1.6 m. below the surface before coming to the one centimeter cut-off. The maximum lateral extension of one spruce root was 13.8 meters before cut-off. Since only a few root systems were excavated, the stunting of spruce roots noted by Siren (1951) was not studied. No intra- or inter-species root grafts were found in excavations of fir and spruce on our study site. The root to shoot ratio will of course be an underestimate since root biomass under one centimeter is not known but an average value (calculated from approximately six randomly chosen plots) for total spruce in spruce stands is approximately .297 and for total fir in fir stands the average is approximately .402.

As for aspen root studies once again the work is basically qualitative (Brendt et al. 1958, Gifford 1964, Tew et al. 1969). The root to shoot ratio average for eight randomly chosen aspen plots was approximately .082. There is no doubt that there is underestimation but without any comparable literature very little can be said. An ANOVA test was conducted on the aspen pit root data. From this test it was found that there was no significant difference between clones (α = .01) in their pit root biomasses. In other words, there was greater variability within than between clones. It must be pointed out that using the average d.b.h. of the four nearest trees to pit center divided by their average distance to pit center does make biological sense as a predictive variable when examined. The root biomass found in a cubic meter pit will be directly related to the size of the surrounding trees (d.b.h.) and their distance from the pit (the farther away the trees are the less the concentration of roots in the pit).

MAI production equations for aspen display a downward trend with higher diameters (Figures 18A-B, 17A-B). While only one or sometimes more than one point showed this downward trend, it seems the trend is incontrovertible due to the heartrot associated with larger aspen trees. This heartrot was found in a number of aspens. Most of the decay was incipient but in the largest aspen it was extensive. Because only a few points showed this definite trend a hand-fitted curve was used to predict the aspen production and a sixth degree polynomial was fit to that curve. This early decline in production fits in with the short life cycle hypothesized by Odum (1969) for species in early successional stages. For fir MAI there was no hint of a downward or leveling trend anywhere in the data (see Figures 14A-B, 15A-B). This might be due to an inadequate sampling of upper diameter trees. Virtually none of the fir trees dissected were found to possess heartrot, though none were chosen in the hope of finding rot. Because of a lack of leveling, standard regression techniques were used. A comparison of aspen and fir bole wood MAI's reveals that up to a d.b.h. of 40 cm. aspen outproduces fir. Past 40 cm., fir according to our equation then outstrips aspen with its declining production. If we put complete faith in our observations we can postulate that the heartrot associated with aspen is the 'valve' that eventually turns off its production, giving fir a chance to dominate the stand.

Spruce MAI, like fir MAI also showed no very definable leveling (Figures 12A-B, 13A-B). The variability in the spruce MAI values seems to be greater than either fir or aspen. It must be admitted that there seems to be one point that consistantly shows a lower value than expected. But, because of the large variability and relatively smaller absolute differences between our highest diameter point and the point sequentially before it, standard statistical techniques were used instead of polynomials. Spruce, in terms of bole wood MAI, seems to be out-producing fir while still not (up until about 40 cm.) out-producing aspen. Of course, after 40 cm., spruce's MAI is greater than that of aspen, whose MAI predicted line, if continued further, would suggest death or a negative production at some future time.

Aspen PAI data shows, in a number of higher diameter points, a clear leveling and downward trend both in bole and branches. The PAI data in aspen as well as the other species seems to show a larger variability than MAI. This greater variability might be associated with the greater sensitivity of PAI to such factors as site and competition. Because of these leveling trends PAI data for aspen were hand fitted and a sixth degree polynomial applied with d.b.h. as the independent variable. Fir bole wood and bark PAI data, like its comparable MAI data, once again shows no leveling (see Figure 20 A-B). Again the trees sampled, their size, and general good condition probably explains the lack of leveling that would be expected. Fir branch wood and bark do however, show some slight leveling (see Figure 21A-B); enough and in a consistent manner that a regression could be applied. Explaining this apparently higher 'sensitivity' of fir branches is not easy. Competition and sampling might be possible answers. It should also be pointed out that PAI is a better indicator of recent trends in production. The reason being that PAI is based on the last ten year's growth whereas any trends that might exist in a tree's life cycle is masked when a grand average is taken to generate a MAI value. Fir bole wood PAI is consistently greater than aspen bole wood PAI. In spite of this, as we shall see later, PAI estimates show fir stands to be producing less than aspen stands. This same stand trend is also shown by MAI estimates. Spruce wood and bark PAI's (Figures 16A-B, 17A-B) all show a leveling and even a downward trend. For bole wood PAI, spruce out-produces fir for most mid and upper diameters. In the case of spruce bole bark we see a very noticable drop for higher diameters. The comparable graph for fir shows a linear relationship. The bark sloughing associated with spruce might be a contributing factor. From the PAI data it seems that fir outproduces spruce in both branch wood and bark. In the field it became evident that fir would normally possess more live branches than a comparably sized spruce (e.g., a fir could have well over 400 branches whereas a similarly sized spruce might have only 200-300).

Total stand biomass along successional time (Figure 26B) seems to display a sharp rise from time zero (meadow) to about 75 years. This time period, of course, corresponds to an aspen dominated stand. It would have been desirable to have a few younger stands in the 10-40 years range, to sharply define the shape of the curve at the lower end. It probably can safely be said though, that biomass incrases curvilinearly during this period. Referring back to Figure 26B, a discernable leveling or at least slower rate of biomass accumulation can be seen during the period from 80 to about 170 years. This period corresponds roughly to a fir dominated stage and, as shall be seen later, a drop in stand production. From about 175 years onward, biomass once again starts to accumulate at a faster rate. The stand biomass data does seem to strengthen Odum's hypothesis that biomass is low in early stages and high in mature stages. It must be noted that this is based only on the wood and bark biomass of the trees. While this will probably be the largest single community component, a more complete test of the hypothesis will have to wait till other community components, such as vertebrate biomass, are measured.

Biomass is also a very good measurement of the size of an organism. Odum hypothesized that the size of an organism will be small in early stages and large in later stages. It becomes clear that based on observations in the field and on the individual tree and stand biomass data, that the hypothesis seems to be true for our trees. By comparing, lets say, the bole wood biomass equations for aspen, fir, and spruce it can be seen that spruce gets to be the largest organism followed by fir and aspen.

If we study the species breakdown of biomass versus age (Figure 27A) we can see the dynamics behind the total stand biomass graph presented before. Aspen totally dominates the stand during the first 80-100 years. Fir and spruce are both present during this time but are in small amounts. Eventually aspen biomass drops off fairly rapidly. The reasons for this drop might be senescence, heartrot, and changing site factors. Whatever they may be they allow fir to eventually dominate. Fir, however, succumbs at about 175 years to spruce. Spruce remained dominant in all the older stands used in our study. Based on this species-breakdown graph we can make a comment on another Odum hypothesis. Odum states that early stage organisms have a short stability, while later stage organisms possess longer stabilities. Using species total biomass dominance as an indication of stability and studying Figure 27A, a number of inferences can be drawn. In terms of actual dominating time spruce seems to be longest. It dominates at about 160 years onward, for a minimum of at least 100 years. Aspen seems to be next, dominating for 80-100 years. Fir seems to be last only truly dominating from 100 years to 160 years, for a total of only about 60 years. Based solely on this criterion, Odum's hypothesis would seem to be wrong since aspen dominates longer than fir, but after a close inspection of spruce dominated stands it becomes evident that aspen is only sporadically found (if at all found) in spruce stands. Fir on the other hand seems to keep a constant biomass in some spruce stands or at least was always present to some degree in the spruce stands measured. Using just persistence as the criterion the evidence seems to generally support the Odum hypothesis (it must be remembered that aspen clones have been found to be as much as 10,000 years old).

Several estimates of above-ground wood and bark stand biomass are available in the literature. These values when compared to our stand estimates from northern Utah show a fairly close correlation for comparable ages. Bray and Dudkiewicz's (1963) estimate for a 38 year old stand in Ontario was 56,000 kg/ha. Peterson et al. (1970) working in a 66-89 stand in Alberta found the above-ground biomass to be 75,500 kg/ha. Pollard (1970), also in Ontario, found a 52 year old stand to have a biomass of 91,800 kg/ha. My values were respectively, 65,000 kg/ha, 82,800 kg/ha, and 128,000 kg/ha.

Whittaker and Niering (1975) sampled a subalpine fir stand in the Santa Catalina mountains with a maximum age of 130 years. Their above ground wood and bark biomass figure of approximately 340 mt/ha is three times the 102 mt/ha figure for our study. The wide difference may be due to the site and difference in stand composition or structure. The Whittaker site has both <u>Abies lasiocarpa</u> and <u>Pseudotsuga menziesii</u>, while this study's plots contained <u>Abies lasiocarpa</u> and <u>Picea engelmannii</u>. Our study always used the tree of maximum age (plus age correlations for time to reach d.b.h. and lag from meadow stage). It could be possible that Whittaker's stands are much older than just the age of the fir would indicate.

Landis and Mogren (1975) found above ground wood/bark value of 310-415 mt/ha for four spruce stands having a maximum age of 250 years. This study's estimate of 336 mt/ha for a comparably aged stand falls right in between the values found by Landis and Mogren.

The data for two separate stand production estimates (MAI and PAI) versus successoinal age (Figure 27B) both show a startling bi-modal distribution. Both methods show stand production peaking at about 75 years, dropping during the 100-200 year period, and again reaching a similar absolute peak at around 260 years.

While our study doesn't present net community production its estimates of net above ground wood and bark production might still shed some light on Odum's (1969) production hypothesis. If a comparison is made, this study's bimodal production curve is in opposition to the high production in early stages and low production in mature stages stated by Odum. Since wood and bark will probably represent the highest biomass and production components in our plots it can be seen that these particular relationships presented will determine the validity of Odum's biomass and production hypotheses. A species breakdown of MAI and PAI versus time (Figure 28A-B) show the dynamics of the situation. In terms of MAI aspen produces more alone than any other species at any other time. It is only when adding the productions of all species on a plot (i.e., spruce at 250 years) that the highly similar total productions in aspen and spruce stands occur (Figure 27B). As time progresses aspen production drops off while fir and spruce production increases. Fir production, however, tends to level off after a while and even drop in some stands starting at about 150 years. Spruce production continues to climb, though never alone reaching the production output of aspen, but eventually outproducing fir. For the PAI species breakdown (Figure 28B) a similar scenario to that of MAI is seen. The difference seems to be in one spruce stand that is producing nearly as much as aspen did alone. It must be noted before going on that the behavior of production beyond the times represented by the plots is unknown. It follows then that a drop in production is possible if not probable beyond the time studied.

An above-ground wood and bark aspen production value of 1.34 mt/ha/yr for a 52 year old stand found by Pollard (1971) is comparable but smaller than the 1.9 and 2.6 mt/ha figure found by this study. Bray et al. (1963) found wood and bark production to be 2.57 mt/ha/yr for a 38 year old stand and 5.71 mt/ha/yr for a 41 year old stand. The extrapolated values from this study are lower ranging from 1.7-2.1 mt/ha. For the 130 year old subalpine fir studied by Whittaker and Neiring (1975) and mentioned earlier in this paper, a net production value for fir alone was about 4.53 mt/ha/yr. Like the biomass figures presented before Whittaker and Neiring's production estimate is again much greater than the 1.2 and 2.1 mt/ha/yr found by this study. Again as stated before site and age are probably the main reasons for these differences.

CONCLUSIONS

Diameter at breast height and its transformations were found to be the best predictors for biomass and production of species' components. Stand above and below-ground wood and bark biomass was found to be low in developmental (aspen) stages (150 mt/ha at 75 years) and high in mature (spruce) stages (520 mt/ha at 258 years). Net aboveground wood and bark production was found to be, by two separate estimates, bimodal over time. Net production was high in developmental stages (2.3-4.8 mt/ha at 75 years), low in mid (fir dominated) stages (1.7-3.0 mt/ha at 130 years), and high again in mature (spruce dominated) stages (2.4-4.8 mt/ha at 260 years).

A comparison with the literature of our biomass and production estimates, for species and stands, proved to be favorable. Based on our findings, and in light of them alone we would accept Odum's hypothesis regarding biomass values over time. We would also tend to support Odum's theories regarding total organic matter, stability, and organism size through succession. We would reject Odum's hypothesis regarding net production on the sole basis of our estimates of production over time.

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A P P E N D I X

Table 5. Aspen biomass data (weight in kg).

DBH (cm)	Bole wood biomass	Bole bark biomass	Branch wood biomass	Branch bark biomass
14.2	24.62	5.190	2.067	2.406
10.9	16.80	4.357	1.250	1.999
4.5	.296	.107	.106	.063
21.0	89.38	19.06	7.652	5.752
30.4	201.07	39.02	20.267	12.097
13.2	28.44	8.681	3.554	2.121
8.3	13.58	3.999	.764	.456
25.6	115.89	30.28	7.069	4.219
48.2	389.54	144.70	61.310	36.595
6.3	36.51	9.231	.268	.160
10.4	18.62	3.768	2.079	1.241
16.5	59.39	14.06	4.091	2.442
21.0	93.82	23.08	7.082	6.814
8.8	6.841	2.002	2.397	1.826
26.1	134.57	30.77	17.960	10.720
34.1	201.1	59.48	20.675	15.542
11.1	21.40	6.087	2.468	1.473
13.9	33.04	9.349	8.316	4.964
19.0	66.24	15.89	6.827	4.075
38.3	324.12	129.94	36.107	21.552
14.4	27.33	6.825	4.775	2.850

Table 6. Fir biomass data (weight in kg).

DBH	Bole wood biomass	Bole bark biomass	Branch wood	Branch bark biomass
15.6	24.06	4.093	11.004	8.272
30.9	160.87	28.998	27.908	20.979
62.4	702.99	128.23	113.491	85.315
10.8	15.24	3.392	2.018	1.517
35.3	*	*	29.789	22.394
46.9	501.99	103.24	66.836	50.243
13.7	22.87	3.694	5.957	4.478
5.3	2.112	.538	1.338	1.006
51.3	534.35	106.26	87.416	65.714
20.3	53.16	9.500	15.778	11.861
25.1	65.69	4.717	15.765	11.851
41.1	297.52	43.91	64.723	48.655
33.2	192.08	32.77	39.231	29.491
58.8	601.08	104.94	98.337	73.923
17.5	49.80	8.842	9.906	7.447
42.9		43.46	36.966	27.789
8.1	4.932	.7473	1.428	1.073
23.1		27.33	14.129	10.621
27.6	138.45	24.04	41.606	31.277

Table 7. Spruce biomass data (weight in kg).

DBH (cm)	Bole wood biomass	Bole bark biomass	Branch wood biomass	Branch bark biomass
28.1	242.780	23.382	21.324	20.930
42.4	397.616	44.583	42.076	33.964
26.7	194.598	21.064	30.682	23.468
35.1	427.203	25.362	46.174	37.249
14.9	*	*	3.046	3.727
34.5	383.723	32.126	25.722	22.447
40.4	376.684	29.349	49.576	39.303
84.6	2423.513	97.800	196.410	142.058
15.2	24.279	3.383	10.060	10.048
26.7			31.981	25.255
48.3	561.664	77.616	44.369	33.236
9.4	8.092	1.753	2.061	2.044
21.1	38.954	9.112	7.002	5.574
25.4	74.228	24.335	10.313	8.791
65.0	1567.153	90.205	150.165	110.316
33.5	480.859	42.034	55.542	44.362
28.7	182.301	40.623	28.175	25.001
18.0	50.392	3.180	9.586	8.185
28.4	*	*	13.344	12.326
11.2	*	*	2.039	2.369
24.13	224.282	16.055	15.680	13.639
19.1	63.310	6.806	6.028	5.955
22.4	128.417	12.293	20.669	18.635
49.0	785.387	55.554	48.645	39.578
35.8	410.340	21.713	49.339	39.752
29.4	177.292	27.681	48.043	40.080
15.2	25.745	8.741	10.935	11.575
16.7	39.452	12.617	16.929	15.733
63.2	868.925	57.644	146.151	108.145
43.9	564.905	53.586	45.274	36.523

Table 7 Continued.

DBH (cm)	Bole wood biomass	Bole bark biomass	Branch wood biomass	Branch bark biomass
55.6	1019.1840	80.327	119.894	88.088
28.4	139.905	15.812	13.013	10.665
56.1	*	*	148.677	111.431
18.0	46.582	4.137	7.215	7.153
20.1	72.098	7.684	12.139	13.331
61.2	1372.650	79.714	*	*

Table 8. Spruce and fir stump and root biomass.

Species	DBH(cm)	Root/stump biomass (kg)
Spruce		
	16.8	23.88
	12.9	9.91
	35.56	73.93
	66.04	650.97
Fir		
	10.16	4.92
	51.31	243.60
	2.5	0.97

Table 9. Aspen root pit biomass (kg).

Clone	Pit #	Root biomass	DBH/Dist (cm/in)
A	1	1.589	4.86
A	2	.636	3.37
A	3	.358	4.13
B	1	.287	2.73
B	2	1.633	8.32
B	3	.775	5.51
C	1	1.555	10.74
C	2	1.271	6.23
C	3	1.867	11.65
D	1	1.735	4.45
D	2	2.578	20.87
D	3	.178	4.50

Table 10. Aspen production data (MAI) (weight in kg/yr).

DBH (cm)	Bole wood MAI	Bole bark MAI	Branch wood MAI	Branch bark MAI
14.2	.821	.173	.093	.056
10.9	.600	.156	.073	.043
21.0	1.568	.334	.167	.129
13.2	.474	.145	.060	.035
8.3	.277	.0814	.016	.009
25.6	1.525	.398	.093	.056
48.2	2.083	.774	.449	.256
10.4	.640	.108	.067	.040
16.5	1.099	.259	.078	.047
21.0	1.737	.427	.161	.096
8.8	.193	.040	.059	.035
26.1	2.403	.549	.385	.233
34.1	2.957	.875	.559	.432
11.1	.412	.117	.071	.042
19.0	1.183	.284	.122	.073
38.3	4.001	1.604	.671	.397
14.6	.719	.180	.126	.075

Table 11. Fir production data (weight in kg/yr).

DBH (cm)	Bole wood MAI	Bole bark MAI	Branch wood MAI	Branch bark MAI
15.6	.415	.071	.223	.167
30.9	1.693	.305	.344	.258
62.5	6.449	1.176	1.833	1.385
10.8	.113	.025	.018	.014
13.7	.369	.060	.099	.074
5.3	.032	.0082	.024	.018
51.3	4.993	.993	1.020	.768
25.1	1.058	.076	.366	.276
41.1	3.067	.453	.890	.669
33.2	1.902	.324	.879	.659
58.8	6.533	1.14	1.607	1.130
17.5	.743	.132	.148	.111
8.1	.073	.011	.022	.017
27.7	1.173	.204	.376	.284
42.9	*	*	.715	.538
23.1	*	*	.156	.117

* data is missing

Table 12. Spruce production data (MAI) (weight in kg/yr).

DBH (cm)	Bole wood MAI	Bole bark MAI)	Branch wood MAI	Branch bark MAI
28.1	1.640	.160	.144	.151
42.4	2.470	.277	.261	.211
26.7	1.046	.113	.165	.126
13.0	2.347	.139	.254	.205
34.5	2.444	.205	.164	.143
40.3	2.528	.197	.333	.264
84.6	8.845	.357	.717	.518
15.2	.225	.031	.093	.093
48.2	2.925	.404	.231	.173
9.4	.052	.011	.013	.013
25.4	.379	.124	.053	.045
65.0	7.758	.447	.743	.456
21.1	.176	.041	.032	.025
33.5	3.082	.269	.356	.284
28.7	.925	.206	.143	.127
18.0	.362	.003	.069	.059
19.1	.405	.044	.039	.038
22.4	.850	.081	.137	.123
49.0	3.83	.271	.276	.226
35.8	2.345	.124	.282	.227
29.5	2.038	.318	.552	.461
15.2	.268	.091	.114	.121
16.8	.647	.207	.278	.258
63.2	4.77	.317	.803	.594
43.9	3.716	.353	.298	.240
55.6	6.661	.525	.784	.576
28.4	.813	.092	.076	.062
18.0	.256	.023	.040	.040
28.1	.632	.069	.106	.117

Table 13. PAI production data (kg/yr).

Species	DBH (cm)	Bole wood PAI	Bole bark PAI	Branch wood PAI	Branch bark PAI
Aspen	13.2	.800	.244	.101	.059
Aspen	25.6	1.731	.449	.106	.063
Aspen	6.3	1.344	.341	.010	.006
Aspen	10.4	1.294	.218	.120	.071
Aspen	8.8	.346	.071	.106	.063
Aspen	26.1	3.122	.710	.417	.249
Aspen	34.1	3.157	.953	.325	.244
Aspen	11.1	.727	.206	.084	.050
Aspen	19.0	2.334	.560	.240	.143
Aspen	38.3	3.422	1.377	.386	.228
Aspen	14.4	1.154	.289	.202	.120
Aspen	48.2	3.200	1.201	.187	.140
Fir	15.6	1.188	.202	.543	.409
Fir	30.9	3.838	.692	.666	.502
Fir	62.4	6.513	1.188	1.065	.794
Fir	10.8	.397	.088	.053	.040
Fir	13.7	1.366	.220	.355	.268
Fir	51.3	7.606	1.513	1.240	.934
Fir	25.1	1.149	.083	.276	.208
Fir	41.1	3.435	.507	.744	.560
Fir	33.2	2.234	.381	.455	.342
Fir	58.8	5.604	.978	.914	.688
Fir	17.5	2.189	.389	.435	.328
Fir	8.1	.224	.034	.065	.049
Fir	27.6	2.847	.494	.856	.645
Spruce	28.1	4.365	.420	.387	.379
Spruce	42.4	2.857	.320	.305	.246
Spruce	26.7	2.065	.223	.328	.250
Spruce	34.5	4.844	.406	.327	.285
Spruce	40.3	6.333	.493	.840	.665

Table 13 Continued.

Species	DBH (cm)	Bole wood PAI	Bole bark PAI	Branch wood PAI	Branch bark PAI
Spruce	84.6	9.642	.389	.792	.572
Spruce	9.4	.115	.025	.030	.030
Spruce	65.0	8.310	.478	.802	.481
Spruce	21.1	.228	.053	.041	.033
Spruce	33.5	5.588	.488	.649	.514
Spruce	28.7	2.858	.637	.446	.395
Spruce	22.4	1.759	.168	.285	.257
Spruce	49.0	8.966	.634	.559	.454
Spruce	35.8	3.818	.202	.463	.372
Spruce	15.2	1.191	.404	.510	.408
Spruce	16.8	1.562	.499	.676	.627
Spruce	63.2	4.387	.291	.737	.290
Spruce	43.9	5.574	.529	.452	.364
Spruce	55.6	8.252	.650	.979	.718
Spruce	28.4	1.092	.123	.102	.084

Table 14. Total stand biomass and production data.

Plot #	Dominant species	Est. age since meadow	Total biomass (kg/ha)	Total MAI (kg/ha/yr)	Total PAI (kg/ha/yr)
211	Aspen	75	162837.982	2875.74	4062.48
213	Aspen	73	175744.960	3175.72	4543.06
214	Aspen	87	146737.912	2234.2	3226.96
215	Aspen	73	150923.986	2671.180	3883.34
221	Aspen	69	132842.106	2348.72	3653.04
223	Aspen	69	173621.14	3363.06	4737.78
224	Aspen	51	90081.038	1994.2	2647.28
225	Aspen	71	143345.96	2817.62	4020.22
311	Fir	229	340049.754	2558.32	3785.18
313	Fir	124	157548.132	1450.6	2367.94
314	Fir	206	314472.216	1842.18	2283.40
315	Fir	147	199656.538	1746.78	2758.52
321	Fir	211	307199.78	1843.2	3431.48
323	Fir	130	220912.024	2056.0	3035.28
324	Fir	220	411458.734	2213.76	3502.64
325	Fir	135	194682.024	1772.98	3003.06
411	Spruce	227	520653.198	2006.74	2672.18
413	Spruce	199	347040.392	1560.38	2350.72
414	Spruce	161	197214.512	1197.32	2031.1
415	Spruce	173	366789.462	1947.86	3192.3
421	Spruce	171	294366.334	1224.5	1971.16
423	Spruce	235	372567.354	1574.86	2243.98
424	Spruce	258	523650.888	2730.62	4859.26
425	Spruce	253	437157.498	2200.14	3175.08