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THE NUTRITIONAL QUALITY OF ASPEN
AS A WINTER AND SPRING FOOD
FOR RUFFED GROUSE IN NORTHERN MICHIGAN

presented by

Bobbi Lee Webber

has been accepted towards fulfillment
of the requirements for

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Jonathan B. Haufler
Major professor

Date August 4, 1987

THE NUTRITIONAL QUALITY OF ASPEN AS A WINTER AND SPRING FOOD FOR RUFFED GROUSE IN NORTHERN MICHIGAN

By

BOBBI LEE WEBBER

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ABSTRACT

THE NUTRITIONAL QUALITY OF ASPEN AS A WINTER AND SPRING FOOD FOR RUFFED GROUSE IN NORTHERN MICHIGAN

By

Bobbi Lee Webber

Ruffed grouse heavily utilize trembling and bigtooth aspen as a food resource during winter and early spring. Abundance and nutritional quality of aspen may be crucial to overwinter survival and reproductive success.

Bud production and nutritional quality of aspen in the Pigeon River Country State Forest of Michigan was investigated in 1985 and 1986. Aspen clones of both species, sexes, and a diversity of ages and stem densities were sampled.

Bud production varied between years for both species. Crude fat content of buds and catkins also varied yearly. Trembling aspen buds were higher in nutritional quality than bigtooth aspen buds. Male flower buds were higher in apparent digestibility than female buds. Flowering male aspen provided the most bird use days/tree.

Habitat managers should perpetuate aspen clones of both species and sexes that are consistant and/or abundant flower bud producers.

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INTRODUCTION

The ruffed grouse (Bonasa umbellus) is the most widely distributed game bird in North America, occurring in 38 states and 13 Canadian provinces. It is considered an important small game resource in 30 of these states and provinces (Gullion 1977). Therefore, it is desirable to maintain quality habitat to provide for recreational hunting opportunities.

The most abundant ruffed grouse populations in North American occur where snow lies on the ground for a substantial portion of the winter and temperatures remain below freezing for weeks or months at a time. Conditions approaching the optimum for ruffed grouse are found mainly across southern Canada, northern Minnesota, Wisconsin, and Michigan, and south through New England, New York, northern Pennsylvania, and portions of the Alleghenies (Bump et al. 1947).

Ruffed grouse are considered to be an omnivorous species, although as an adult, only 1.1% animal material is taken in comparison to 98.9% vegetable material (Bump et al. 1947). In New York, 414 plant items have been identified in stomach contents, consisting of representatives of 65 families and over 334 species (Bump et al. 1947). Ruffed grouse are therefore primarily vegetarians, browsing on the buds, twigs, leaves, and fruits of various forest plants, shrubs, and trees. When the ground is bare of snow, ruffed grouse feed on a wide variety of green leaves, fruits, and some insects. When snow covers the ground these birds are almost exclusively dependent on dormant buds, particularly the flower and vegetative buds of trembling (*Populus tremuloides*) and bigtooth (*P. grandidentata*) aspen, and to a lesser extent, the vegetative buds and catkins from species such as birch (*Betula* spp.), cherry (*Prunus* spp.), ironwood (*Ostrya* spp.), and beaked hazel (*Corylus cornuta*) (Bump et al. 1947; Gullion 1967).

Ruffed grouse are dependent upon aspen as a winter and early spring food resource. Stollberg and Hine (1952) found that trembling aspen leaves and buds constituted the most common species in terms of percent total volume and percent occurrence in a fall collection of grouse crops in Wisconsin. In Minnesota, studies of winter and spring feeding activities have shown an almost exclusive dependence upon the flower buds of male aspen (Gullion 1967). McGowen (1973) has reported that buds and twigs of trembling aspen and various species of willows (*Salix* spp.) were the most heavily utilized foods during the winter season in Alaska. Phillips (1967) has also reported aspen as an important fall and winter food of ruffed grouse in northern Utah.

Korschgen (1966), in summarizing ruffed grouse food habits studies, emphasized the importance of aspen as a winter food resource to ruffed grouse throughout its range north of 40 degrees latitude and east of 66 degrees longitude.

It has also been shown that ruffed grouse use aspen buds and catkins as a primary food source 2 to 6 weeks after snow melt in spring (Bump et al. 1947; Godfrey 1967; Svoboda and Gullion 1972). Crop content analysis in Maine (Brown 1946) has shown that buds of trembling and bigtooth aspen are utilized in spring in even greater amounts (71.4%) than during winter. Therefore, the utilization of aspen buds extends into the period when hens begin egg laying. The use of aspen leaves during incubation has also been documented in Minnesota (Maxon 1974).

The importance of this tree species as a habitat component is further suggested by the fact that the distribution of ruffed grouse in the United States and Canada closely parallels that of aspen. Only in warmer climates, where grouse encounter less severe winter conditions, do they persist in the absence of aspen, and there they seldom approach the widespread abundance found in more northern regions where aspen is a prevalent component of the forest composition (Gulllion and Svoboda 1972). Consequently, although ruffed grouse are known to utilize a diversity of food items, throughout their primary range, aspen appears to be the most important plant contributing to their yearlong welfare.

Several factors may contribute to the advantages availed to grouse in utilizing aspen buds as a winter and spring food resource. The physical characteristics of the aspen twigs and the arrangement of the flower buds seem to be important. The twig is rigid, providing the feeding bird with a firm hold, eliminating much fluttering and balancing. The twigs usually enter the fall season with 6 to 8 easily detached flower buds near the tip. This bud arrangement is such that from a single position a bird can take its meals quickly and quietly. Ruffed grouse have been observed taking flower buds at a rate exceeding 45/minute, and birds feeding in aspen seldom spend more than 15 to 20 minutes collecting 90 to 100 g of buds (Gullion and Svoboda 1977). It is of great survival advantage to these birds to feed rapidly and with a miminum amount of commotion as morning and evening feeding activities coincide with the early foraging flights of avian predators.

The nutritional quality of aspen flower buds may also influence survival through physiological mechanisms. Examinations of ruffed grouse carcasses collected during the fall and winter months indicate very little visible fat, with no marked seasonal increase in lipids being observed (Thomas, Lumsden, and Price 1975). Therefore, stored lipids do not appear to be of great metabolic importance to ruffed grouse, supporting an hypothesis that energy supplied by aspen may be a limiting factor to these birds during the winter. Previous research (Doerr 1973) suggested that ruffed grouse select aspen buds with the highest protein levels implicating protein as also being an important nutritional requirement during winter.

The ruffed grouse has long been considered a "cyclic" species, although the factors affecting the often dramatic changes in ruffed grouse population densities and mechanisms by which these factors operate have proven somewhat elusive to biologists (Gullion 1970). Several hypotheses for the cyclic declines in grouse numbers have been proposed, including predation, disease, sunspot activity, and weather (Criddle 1930; DeLury 1930; Ritcey and Edwards 1963), although none of these postulations have been conclusive. Most recently, it has been suggested that annual variations in ruffed grouse food resources may in some way be responsible for changes in grouse densities between years. Gullion (1969) has suggested that the availability of flower buds of trembling and bigtooth aspen largely determines the distribution of breeding grouse. Periodic fluctuation in the nutrient content of aspen buds, tree age, density, thrift, sex, levels of secondary compounds, as well as periodicity of bud production may all influence population cycles, or at least the magnitude of the peaks and troughs of these cycles.

Current habitat management techniques for ruffed grouse are designed primarily to enhance the cover requirements throughout the life cycle. As aspen appears to be a critical food resource during winter and spring seasons throughout the northern range of ruffed grouse, specific management for food resources would appear to be beneficial. An important first step in developing specific management recommendations for aspen as a food resource is the quantitative evaluation of nutritional quality. The objectives of this study were to 1) Determine if sex of dormant aspen flower buds can be differentiated based on bud size, 2) Evaluate the nutritional quality of male and female flower buds, catkins, vegetative buds, and leaves of trembling and bigtooth aspen, 3) Determine if yearly fluctuations in nutritional quality occur, and 4) Determine if yearly fluctuations in abundance of flower buds occurs.

STUDY AREA DESCRIPTION

The study area was the Pigeon River Country State Forest which is located in parts of Cheboygan, Montmorency, and Otsego counties in northern lower Michigan (Figure 1). The 37652 ha forest has a topography consisting of moranic uplands, steep moranic slopes, sandy outwash plains, and river bottoms. The podzol soils of the area range from highly fertile organic soils in the swampy areas to dry sandy soils on the outwash plains. Medium fertility soils are found on the till plains and moraines (Moran 1973).

The forest is composed of a variety of cover types. Coniferous swamps are dispersed throughout the forest and contain tree species such as spruce (*Picea* spp.), northern white cedar (*Thuja occidentalis*), balsam fir (*Abies balsamea*), and tamarack (*Larix laricina*). Upland cover types include mixed and pure stands of aspen (*P. tremuloides* and *P. grandidentata*), maple (*Acer* spp.), beech (*Fagus grandifolia*), basswood (*Tilia americana*), cherry (*Prunus* spp.), birch (*Betula* spp.), jackpine (*Pinus banksiana*), red pine (*P. resinosa*), and white pine (*P. strobus*) (Ficher 1939).

The typical climate of the area is characterized by long cold winters, short cool summers, mild autumns, and

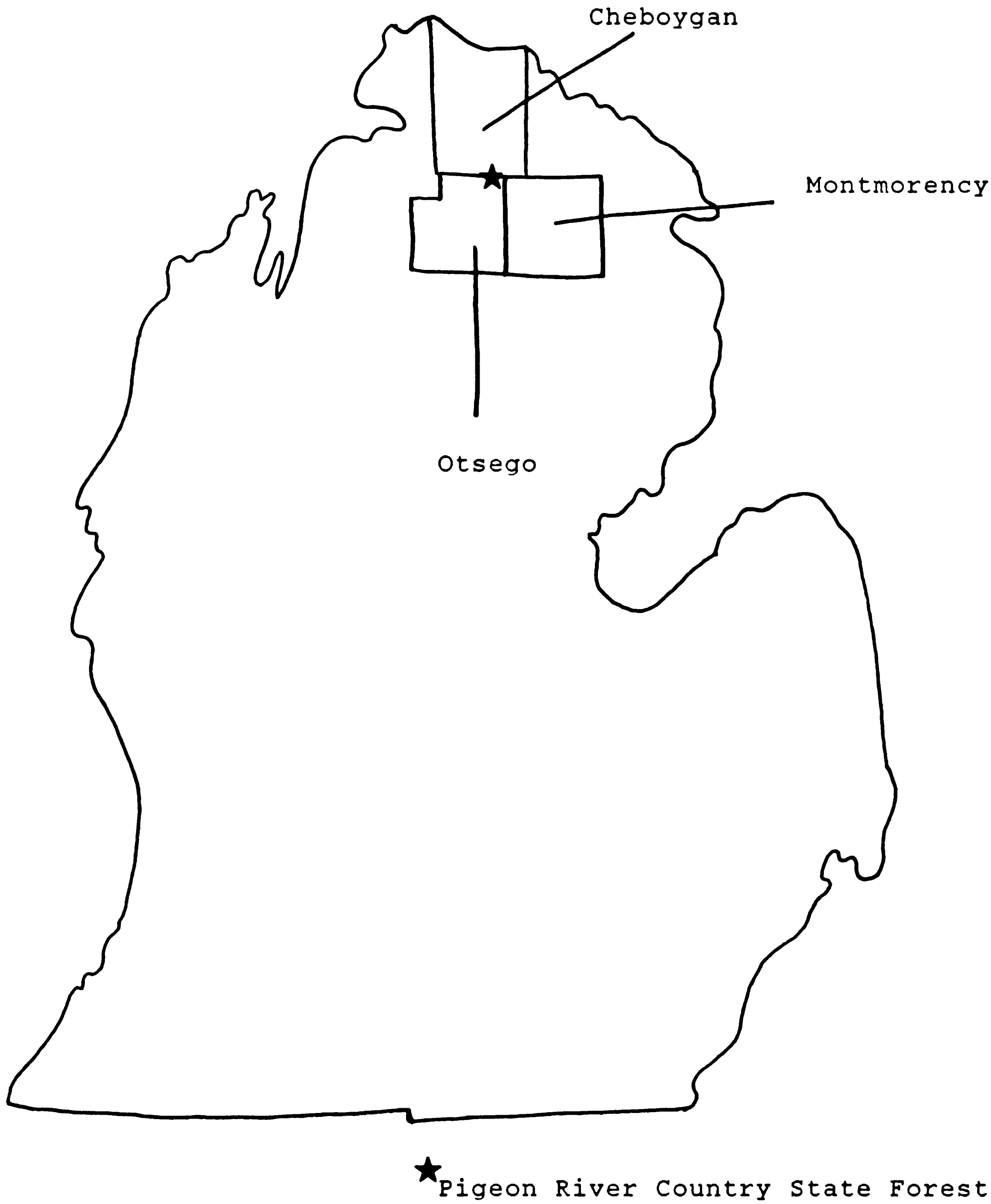

Figure 1. Location of the Pigeon River Country State study area in Cheboygan, Montmorency and Otsego counties of Michigan.

late cold springs. The growing season over the study area is approximately 77 days. Temperatures average -8.0 ^{o}C in January and 19^{o}C in July. Average annual precipitation is approximately 71 cm. Total average snowfall is 290 cm.

MATERIALS AND METHODS

VEGETATIVE SAMPLING

Within the study area clones of both trembling and bigtooth aspen were selected for vegetative sampling. Aspen clones vary considerably in genetic traits such as leaf morphology, seasonal coloring, stem form, branching habit, growth rates, bark characteristics, sex, and phenology (Barnes 1964). The characteristics useful for clone delineation by seasons have been outlined by Barnes (1969) (Appendix, Table 9). The techniques and suggestions of Barnes (1969) were used to delineate aspen clones on the study area. Clones were identified and marked in the fall of 1984 and spring and fall of 1985.

Delineation between the sexes was accomplished during the winter by the use of a disecting microscope. The presence of pollen sacks indicated that flower buds were male, and conversely the absence of pollen sacks indicated that the flower buds were female. Sex was subsequently confirmed in the field during spring at time of flowering.

All trees within an aspen clone are genetically and chemically the same (Blake 1963), therefore, 1 tree was selected within each clone for sampling, and was considered to be representative of the entire clone. Both vegetative and flower buds were collected during winter sampling. Catkins were taken during spring sampling. In addition, leaves were collected in the spring of 1985, during the time when ruffed grouse were involved in incubation activities.

All trees used for vegetative sampling were felled. Samples were collected randomly from throughout the entire tree. For small trees (d.b.h. < 5") all buds, catkins, or leaves were removed. For large trees (d.b.h. > 5"), a composite sample was taken from throughout the entire tree.

For each tree sampled, d.b.h. and tree height were measured. Stem density was measured for each clone by counting all stems greater than 2.54 cm d.b.h. in a 10 x 10 m area centered in the clone. A cross section of each tree was collected for determination of age. These were sanded smooth, and a phenoglucinol dye was added to illuminate the rings. The presence of heart rot in many of the trees impeded highly accurate age determination, although it is felt that tree ages were accurate to within 5 years.

Bud production was estimated during the winter of each sampling year. Production estimates were made both in terms of the number of identified clones flowering, as well as the number of buds produced per sampled tree. During the winters of 1985, 1986, and 1987 each identified clone was checked to determine if flowers were produced, thereby determining the percentage of clones flowering. During the winters of 1985 and 1986, the number of flower buds produced per tree was estimated from trees used for nutritional sampling. For small trees (d.b.h. < 5"), all buds on the tree were collected, and bud production was estimated by total bud counts. On larger trees (d.b.h. > 5"), total sample collection was not possible due to large losses of buds when the tree was felled, therefore an estimation technique was developed. This technique involved first counting the total number of main branches extending from the bole of the tree. Once the tree was felled, the total number of short shoots was counted on every third main branch, thereby giving an estimate of the average short shoots per main branch. A random subsample of 10 of these short shoots was then taken to determine the average number of buds per short shoot. Total bud production was calculated by multiplying:

total branches X average number of short shoots/branch X average buds/short shoot

Checks were made on several d.b.h sizes, and the accuracy of the technique was found to be within 10%.

Average bud weight of flower and vegetative buds was determined as a means of comparing the quantity of food available between the 2 types of buds. Average weights of vegetative buds were determined from a subsample of 100 buds, and a subsample of 200 buds was used for flower buds.

At the time of collection samples were placed in large plastic bags. Once in the laboratory, samples were kept frozen until subsequent analysis. Samples were then dried in a gravitational oven at 50.4^{o}C until they reached constant weight. Dried samples were ground in a Wiley Mill to pass a 1 m sieve and stored in whirl paks until time of analysis.

CHEMICAL ANALYSIS

All vegetative samples were analyzed for the following nutritional components: %dry matter (%DM), %ash, %crude fat, %crude protein , neutral detergent fiber (%NDF), acid detergent fiber (%ADF), acid detergent lignin (%ADL), and caloric value (kcal/g). When there was insufficient vegetative material for all analyses priority was assigned in the following order: %DM, %crude protein, %crude fat, caloric value, %ADF, %ADL, %NDF.

Ash content and %crude fat were determined by methods described in AOAC (1975). Crude fat methods were modified by weighing ground samples into tared filter paper `packets' instead of thimbles. This allowed for a larger number of samples to be analyzed per extraction.

To determine %DM of a sample, 1.0 - 1.1 g of dried ground sample was weighed into pretared porcelain crucibles and oven dried at 100^{O}C for 24 hours. After drying, samples were cooled in a desicator and reweighed. The original sample weights used in all analyses were multiplied by this percentage in order to determine the actual amount of vegetation used.

Total nitrogen was determined by Kjeldahl digestion (AOAC 1975). Samples were digested on a Tecator Block Digestor, model DS-40 (Tecator, Inc. Boulder, Co), in concentrated sulphuric acid at 380^{O}C. Values were obtained using a Technicon Autoanalyzer II (Technicon Industrial Systems, Tarrytown, N. Y.). Crude protein values were determined by multiplying total Kjeldahl N values times 6.25 (AOAC 1975).

Fiber analysis (%NDF, %ADF, %ADL) were conducted according to the procedures of Goering and Van Soest (1970). Hemicellulose, cellulose, and lignin are the cell wall constituents (CWC) determined through NDF analyses. Cell soluble material (CSM) consisting of soluble carbohydrates, starches, organic acids, proteins, and pectin were determined by subtracting CWC values from 100 (Goering and VanSoest 1970). Hemicellulose values were calculated by subtracting ADF from NDF values. Cellulose content was calculated by subtracting ADL from ADF values.

Caloric value of samples was determined by the use of a Parr adiabatic calorimeter (Parr Instrument Co., Moline Ill.). This instrument measures the amount of heat released when a 1.0 g sample of plant tissue is completely oxidized. The plant sample is placed in a combustion chamber which contains excess oxygen. The combustion chamber is immersed in an insulated water jacket and ignited. The temperature rise in the surrounding water is proportional to the samples chemical energy content.

Quality control of the nutritional analysis were checked by running duplicates for 10% of the samples. Any duplicate samples that were not within 10% of the first sample were retested. In addition, any sample yielding what appeared to be spurious results were retested.

DATA ANALYSIS

To test for nutritional differences between years, sexes, and species, the Mann-Whitney U nonparametric test was used (Siegel 1956). The Mann-Whitney U was also used to test for bud size differences between male and female dormant flower buds and vegetative buds.

RESULTS

FLOWER BUD WEIGHTS

Average flower bud weight calculated for male trembling aspen trees was 0.099 g and for female trembling aspen trees was 0.050 g. Analysis of the data indicate that there was a statistically significant difference ($p \leq 0.01$) in bud weight between male and female dormant flower buds. However, the range of bud weights was found to overlap. Males ranged in weight from 0.034 g to 0.172 g, and females ranged in weight from 0.028 g to 0.077 g.

BUD PRODUCTION

In 1985, 65 trembling and 46 bigtooth aspen clones were identified and marked. Of the trembling aspen clones identified, 18 or 27.7% contained flower buds, and of the bigtooth aspen clones identified 18 or 39.1% flowered. The sex ratio for the trembling clones was 1.2 males to 1.0 females, for bigtooth clones the sex ratio was 5.0 males to 1.0 females.

In 1986, 76 trembling and 56 bigtooth aspen clones were identified. Of the trembling aspen clones identified, 44.7% contained flower buds. In contrast, 28.8% of the bigtooth aspen clones produced flower buds in 1986. Sex ratios were 4.0 to 1.0 for trembling and 4.5 to 1.0 for bigtooth.

In 1987, 95 trembling and 61 bigtooth aspen clones were identified. Only 6.3% of the trembling aspen clones flowered, and 15.0% of the bigtooth aspen clones flowered. Sex ratios in 1987 were 0.66 to 1.0 for trembling aspen and 1.33 to 1.0 for bigtooth aspen.

In addition to the number of clones flowering the number of flower buds on the sampled trees within each clone was also estimated. Data indicate that bud production per tree was higher in 1986 than 1985 for both species (Table 1).

Correlations between bud production and site quality, stem density, age, and d.b.h. were examined to determine the factors which may influence yearly variations in bud production. In all cases, however, no strong relationships were observed between these variables.

NUTRIENT COMPOSITION

The nutrient composition of both species of aspen were compared in several ways. Yearly comparisions of nutritional quality were made for aspen vegetative buds, and both sexes of aspen flower buds and catkins. Comparisons of nutritional quality were also made between sexes and between species. When making comparisons of nutritional quality between years, comparisons were made between samples

Table 1. Flower bud production for trembling and bigtooth aspen in the Pigeon River Country State Forest of Michigan during 1985 and 1986.

Species	Year	Mean	Range	Standard Error	Significance of Yearly Differences
Trembling Aspen					
Male	1985(n=9)	1288	275-3232	296	0.01
	1986(n=29)	3524	610-9890	454	
Female	1985(n=3)	1714	591-2720	617	0.05
	1986(n=7)	2503	1222-3896	388	
Bigtooth aspen					
Male	1985(n=7)	852	271-2412	286	0.01
	1986(n=7)	2589	526-5328	634	

collected from the same clones each year. Aspen catkin samples were the only exception to this. For aspen catkins we were unable to sample the same clones each year, therefore a random sample of different clones was used to test for differences between years.

YEARLY FLUCTUATIONS

Differences between years in the nutrient composition of trembling and bigtooth aspen flower buds are shown in Table 2. For trembling aspen male flower buds, the only significant differences found between years were in %crude fat. Percent crude fat was significantly higher in 1985 than 1986. For bigtooth aspen male flower buds %crude protein and %cellulose were the nutrients that varied between years. Percent crude protein was significantly higher in 1986 than 1985, and % cellulose was significantly higher in 1985 than 1986. Sample size of trembling and bigtooth aspen female flower buds were not sufficient to make statistical comparisons.

Trembling and bigtooth aspen vegetative buds also showed yearly variations in %crude fat and %crude protein (Table 3). No significant differences were found between years in the fiber components, %ash, or caloric value of trembling vegetative buds, however a highly significant difference was found for %crude protein. Protein levels were higher in 1986 than 1985. For bigtooth aspen vegetative buds, significant differences were found in both %crude fat

Table 2. Summary of significant differences between years in the nutrient composition of male trembling and male bigtooth aspen flower buds collected in the Pigeon River Country State Forest of Michigan in 1985 and 1986.

	Male Trembling Aspen			Male Bigtooth Aspen		
Nutrients	1985	1986	Significant Differences Between Years	1985	1986	Significant Differences Between Years
% Ash	2.50	2.27	N.S.	2.81	2.63	N.S.
% NDF	59.19	59.12	N.S.	58.91	55.56	N.S.
% ADF	46.01	46.49	N.S.	42.61	42.73	N.S.
% ADL	26.18	27.52	N.S.	22.71	23.52	N.S.
% Hemicellulose	13.18	12.55	N.S.	15.58	12.68	N.S.
% Cellulose	19.94	18.97	N.S.	19.90	18.54	*
% Crude Fat	19.63	17.61	*	15.04	12.24	N.S.
% Crude Protein	10.43	10.66	N.S.	10.08	11.96	*
Caloric Value (K cal/g)	4.67	4.81	N.S.	4.49	4.63	N.S.

N.S. not significant
* significant ($P \leq .05$)

Table 3. Summary of significant differences between years in the nutrient composition of trembling and bigtooth aspen vegetative buds collected in the Pigeon River Country State Forest of Michigan in 1985 and 1986.

	Trembling Aspen			Bigtooth Aspen		
	Mean		Significant Difference	Mean		Significant Difference
Nutrients	1985	1986	Between Years	1985	1986	Between Years
% Ash	2.46	2.45	N.S.	3.68	3.83	N.S.
% NDF	58.76	56.08	N.S.	66.20	64.40	N.S.
% ADF	47.69	47.25	N.S.	52.84	50.63	N.S.
% ADL	31.60	32.37	N.S.	30.58	29.15	N.S.
% Hemicellulose	11.07	8.82	N.S.	13.36	13.54	N.S.
% Cellulose	16.10	14.87	N.S.	22.26	21.77	N.S.
% Crude Fat	25.19	20.98	N.S.	12.92	7.12	*
% Crude Protein	5.82	8.87	**	5.65	8.53	*
% Caloric Value (Kcal/g)	5.04	5.06	N.S.	4.60	4.69	N.S.

N.S. not significant
* significant ($P \leq .05$)
** highly significant ($P \leq .01$)

and %crude protein. Percent crude fat was significantly higher in 1985 than 1986, and %crude protein was higher in 1986 than 1985.

For both male and female trembling aspen catkins, the only statistical differences observed between years was in %crude fat (Table 4). For both sexes %crude fat was significantly higher in 1985 than 1986. For male bigtooth aspen catkins, highly significant difference were found between years in %crude fat, and all fiber components except %hemicellulose (Table 5). Percent NDF, %ADF, %ADL, %cellulose, and %crude fat were all significantly higher than 1986.

DIFFERENCES BETWEEN SEXES

Data from 1985 and 1986 were combined to make comparisons between sexes. Flower buds from male trembling aspen were significantly higher in %crude fat and caloric value (Table 6). Female flower buds were significantly higher in all fiber components except %hemicellulose. No significant differences were found to exist for %crude protein between sexes. Several differences were found between male and female trembling aspen catkins (Table 6). Females were found to be significantly higher in %crude protein and all fiber components except %hemicellulose. No significant differences were found in %crude fat, %ash, % hemicellulose, or caloric value. Sample size of bigtooth

Table 4. Summary of significant differences between years in the nutrient composition of male and female trembling aspen catkins collected in the Pigeon River Country State Forest of Michigan in 1985 and 1986.

	Male Trembling Aspen	Female Trembling Aspen
Nutrients	Significant Differences Between Years	Significant Differences Between Years
% Ash	N.S.	N.S.
% NDF	N.S.	N.S.
% ADF	N.S.	N.S.
% ADL	N.S.	N.S.
% Hemicellulose	N.S.	N.S.
% Cellulose	N.S.	N.S.
% Crude Fat	**	*
% Crude Protein	N.S.	N.S.
% Caloric Value (Kcal/g)	N.S.	N.S.

N.S. not significant
* significant ($P \leq .05$)
** highly significant ($P \leq .01$)

Table 5. Summary of significant differences in the nutrient composition of male bigtooth aspen catkins collected in the Pigeon River Country State Forest of Michigan in 1985 and 1986.

	Male Bigtooth aspen
Nutrients	Significant Differences Between Years
% Ash	N.S.
% NDF	**
% ADF	**
% ADL	**
% Hemicellulose	N.S.
% Cellulose	**
% Crude Fat	**
% Crude Protein	N.S.
Caloric Value (Kcal/g)	N.S.

N.S. not significant
** highly significant ($P \leq .01$)

Table 6. Summary of significant differences in nutrient composition between male and female trembling aspen flower buds and catkins collected in the Pigeon River Country State Forest of Michigan in 1985 and 1986. (Sex under which nutrient is listed has the greater value.)

	Female Trembling Aspen		Male Trembling Aspen	
	Nutritional Component	Significant Differences Between Sexes	Nutritional Component	Significant Differences Between Sexes
Flower Buds	% NDF	**	% Crude Fat	*
	% ADF	**	Caloric Value (Kcal/g)	**
	% ADL	**		
	% Celulose	**		
Catkins	% NDF	**		
	% ADF	**		
	% ADL	**		
	% Crude Protein	**		
	% Celulose	*		

* significant ($P \leq .05$)
** highly significant ($P \leq .01$)

aspen female flower buds and catkins were not sufficient to make comparisons between sexes of that species.

DIFFERENCES BETWEEN SPECIES

When making comparisons between species, data from 1985 and 1986 were again combined. Several differences were found between species in flower buds, vegetative buds, and leaves (Table 7). Trembling aspen flower buds were significantly higher in caloric value and all fiber components except %hemicellose. Bigtooth aspen flower buds were significant higher in %hemicellulose, %crude protein and %ash. No significant differences were found between species for %cellulose. For trembling and bigtooth aspen vegetative buds, highly significant differences were found between species for all nutritional components. Bigtooth aspen vegetative buds were higher in all of the fiber components except %ADL. Trembling aspen vegetative buds were higher in %ADL, %crude fat, %crude protein, and caloric value. Leaves collected from both species showed no siginificant differences in %NDF and %crude fat. However, bigtooth aspen leaves were found to be significantly higher in %ash, %crude protein, %hemicellulose, and %cellulose. Trembling aspen leaves were significantly higher in %ADF, %lignin, and caloric value.

The greatest overall variation in nutrient content of all materials assayed was found between male trembling aspen

Table 7. Summary of significant differences in nutrient composition between trembling and bigtooth aspen flower buds, vegetative buds and leaves collected in the Pigeon River Country State Forest of Michigan in 1985 and 1986. (Species under which nutrient is listed has the greater value.)

	Trembling Aspen		Bigtooth Aspen	
	Nutrient Composition	Significant Differences Between Species	Nutrient Composition	Significant Differences Between Species
Flower Buds	% NDF	**	% Ash	**
	% ADF	**	% Hemicellulose	*
	% ADL	**	% Crude Protein	*
	Caloric Value (Kcal/g)	**		
Vegetative Buds	% ADL	**	% NDF	**
	% Crude Fat	**	% ADF	**
	% Crude Protein	**	% Ash	**
	Caloric Value (Kcal/g)	**	% Hemicelulose	**
			% Cellulose	**
Leaves	% ADF	**	% Ash	**
	% ADL	**	% Crude Protein	*
	Caloric Value (Kcal/g)	**	% Hemicellulose	**
			% Cellulose	*

* Significant ($P \leq .05$)
** Highly Significant ($P \leq .01$)

and male bigtooth aspen catkins. Because of these variations, data from 1985 and 1986 were not combined for comparisions, and were analyzed separately. Table 8 summarizes the differences between species for trembling and bigtooth aspen catkins. In 1985, the only significant differences found between the species were in %crude fat and %crude protein. Trembling aspen catkins were significantly higher in %crude fat, and bigtooth catkins were significantly higher in % crude protein. In 1986, significant differences were found in all of the fiber components accept %hemicellulose. Trembling catkins were significantly higher in %NDF, %ADF, %ADL, and %cellulose. Bigtooth catkins were significantly higher in %ash, and %crude protein. No significant differences were found between species for %crude fat, %hemicellulose, or caloric value.

The means, standard errors and ranges by year for nutritional components, bud weights, and ages of the trembling aspen and bigtooth aspen trees sampled are listed in Tables 10-13 in the Appendix.

BIRD USE DAYS

One value of Standard Metabolic Rate (SMR) has been reported in the literature for ruffed grouse. Brander and Rasmussen (1973) determined that the SMR for a 644g ruffed grouse was 46.1 kcal per day, assuming a respiratory quotient (RQ) of 0.80. It was felt that the size of a

Table 8. Summary of significant differences in nutrient composition between trembling and bigtooth aspen catkins collected in the Pigeon River Country State Forest of Michigan in 1985 and 1986. (Species under which nutrient is listed has the greater value.)

	Trembling Aspen		Bigtooth Aspen	
	Nutrient Composition	Significant Differences Between Species	Nutrient Composition	Significant Differences Between Species
1985	% Crude Fat	**	% Crude Protein	**
1986	% NDF	**	% Ash	*
	% ADF	**	% Crude Protein	**
	% ADL	**		
	% Cellulose	**		

* significant ($P \leq .05$)
** highly significant ($P \leq .01$)

particular food item could greatly influence the nutritional value of that food item for ruffed grouse. Therefore, the number of individual food items required to produce 46.1 kcal of gross energy was calculated. This value was then used to calculate the average bird use days/tree for bud types of both species. For flower buds, separate calculations were made for 1985 and 1986 as flower bud size appeared to vary between years for both species. Veg. bud size appeared to remain constant between years.

In 1985, approx. 2.5 times more trembling aspen female flower buds than trembling male flower buds would have been needed to supply the energy required to maintain SMR for 1 day. Approximately 2.3 times more trembling aspen vegetative buds would have been needed compared to trembling aspen male flower buds. In 1986, 3.5 times more trembling female aspen flower buds, and 9.5 times more trembling aspen vegetative buds than male flower buds were needed to supply 46.1 kcal of energy per day.

In 1985, comparisions between male and female bigtooth aspen flower buds could not be made due to the lack of flowering female trees. However, 1.70 more bigtooth aspen vegetative buds than bigtooth male flower buds were needed to produce 46.1 cal gross energy in 1985. In 1986, approximately 5.0 times more bigtooth female flower and 5.0 times more vegetative buds than male flower buds were required to supply the energy needed to support 1 ruffed grouse at SMR.

Bird use days/tree was calculated by dividing average bud production for sampled trees by the average number of buds required to produce 46.1 kcal energy/day. For vegetative buds, bird use days per tree did not vary between years. For trembling aspen vegetative buds an average of 2.15 days per tree in 1985 was calculated. This was only slightly lower than 2.69 days per tree calculated for 1986. For bigtooth aspen vegetative buds 2.07 bird use days in 1985 and 1.93 bird use days in 1986 were calculated. Male trembling aspen trees had the highest average bird use days at 5.10 days per tree in 1985 and 25.53 days per tree in 1986. These figures are almost twice those of female trembling aspen trees in 1985, and triple those of female trembling aspen trees in 1986. A similar trend was also seen for bigtooth aspen. Males had an average value of 14.20 bird use days/tree, twice that of 7.74 for female bigtooth aspen in 1986.

DISCUSSION

Previously, sex in dormant aspen flower buds has been determined based on visual bud size, with the larger flower buds being sexed as males and the smaller flower buds as females. Our work indicates that male and female buds overlap in size, although males on the average will be larger. It is therefore felt that sex determination based on bud size is not an entirely accurate technique, and alternate techniques should be used. Lester (1963), determined that by mid August floral differentiation and development in aspen has reached a condition where only the physiological requirement of cold treatment must be met before floral maturity can occur. Under natural conditions flower buds are physiologically ready for development by mid December or January. Therefore, for a period of approximately 8 months, from mid August to mid April, sex can be determined by microscopically examining floral structures. At these times the pollen sacks and stamen primordia of male buds are easily seen when the bud is sliced in half and placed under a microscope. A light microscope is required to see these structures from August to mid December or January. From January until floral elongation in April only a dissecting microscope or hand lens is required.

Aspen trees begin flowering at 10 to 20 years of age, and flower production varies from light to heavy crops on cycles of 3 to 5 years (Brinkman and Roe 1975). Data from this study indicate that the number of clones flowering, as well as the number of flower buds produced per tree varies between years. The factors influencing bud production, both in terms of the number of clones producing flower buds, as well as the number of flower buds produced per tree have not yet been determined. Relationships between age, stocking density, site quality, and bud production were evaluated, but no strong relationships were observed.

Yearly weather conditions and variations as well as genetic inheritance may be the factors influencing bud production. Weather has been shown to have an important influence on carbohydrate production and subsequent reproductive primordia development in douglas fir (Pseudotsuga menziesii) (Ebell 1971). Morris (1947) has stated that weather conditions during the growing season influence the carbon-mineral nutrient ratio of balsam fir, and thus affects bud production. Apparently there is a correlation between hot, dry years, which favor photosynthesis rather than uptake of minerals, and heavy seed years immediatley following for balsam fir. This process may also be true for aspen as the nutritional status of many plants is an important aspect of floral production. Flowering parts of plants are particularly dependent on availability and translocation of nutrients. The carbon:nitrogen ratio has been shown to be extremely influential in flower production in many dioecious species (Copeland 1976).

The genetic make up of aspen clones may also be an important component influencing flower production as well as flowering periodicity. In controlled experiments with aspen, Valentine (1975) found strong genetic control of sex ratio and earliness of flowering. His studies have indicated that genetics may influence flowering frequency as well. His study also showed that male trees flower more frequently and at a younger age than do female trees. Further studies such as Valentine's are needed to more fully evaluate the genetic control of flowering frequency. Based on information collected from other species, it can be speculated that yearly weather conditions and genetic differences between clones may be the factors ultimately influencing yearly bud production in aspen as well.

The nutritional data from this study indicate that %crude protein and %crude fat vary between years for flower buds, vegetative buds, and catkins. Huff (1973) in Minnesota also found wide year to year variations in the levels of %crude fat for male trembling and bigtooth aspen flower buds. Both protein and energy may play an important role in over-winter survival and/or subsequent body condition in the spring. The level of protein in the diet may have an important influence on body condition, and protein has been shown to affect many aspects of reproductive success in captive ruffed grouse (Beckerton and Middleton 1982). For female red grouse (Lagopus lagopus scoticus) dietary nitrogen has been shown to be particularly important in establishing the "nutritive condition" and subsequent breeding success (Moss, Watson, and Parr 1975). Thomas et al. (1975) determined that ruffed grouse have low body reserves of lipids and glycogen, and large reserves of protein during winter months. Under adverse winter conditions grouse may deplete these limited energy reserves and thus have to utilize body protein as an energy source (Beckerton and Middleton 1983). As a consequence of winter protein catabolism, birds could potentially enter the breeding season with suboptimal protein reserves. Field observations (Maxon 1974) have indicated that aspen is a preferred food source at least during the pre-incubation and incubation periods. The continued use of aspen buds and catkins in the spring may be related to a need to increase nitrogen retention as ovarian recrudescence occurs. In evaluating the effects of 5 levels of dietary protein on body weight, food consumption, and nitrogen balance of ruffed grouse throughout the breeding cycle, Beckerton and Middleton (1983) have shown that females consuming foods with high protein levels maintained better physiological condition than those with low dietary protein levels.

Studies of ruffed grouse population cycles since 1958 at Cloquet, Minnesota conclude that the periodic fluctuations in grouse populations are not entirely the result of any "die-off", as they are the failure to recruit young birds each season to replace those lost through "normal" attrition (Gullion 1970). Therefore, in addition to the role aspen buds may play in the overwinter survival of ruffed grouse, the nutritional plane in which these birds enter the breeding season and their subsequent breeding and brood rearing success may be equally influenced.

Yearly variations in levels of %crude fat may also have an important role in body condition of ruffed grouse. Examinations of ruffed grouse carcasses collected during the fall and winter months indicate very little visable fat, with no marked seasonal increase in lipids being observed (Thomas et al. 1975). Therefore, stored lipids do not appear to be of great metabolic importance to ruffed grouse, particularly during the winter months, supporting the hypothesis that energy supplied by aspen may be a limiting factor to these birds during the winter. Percent crude fat is a measure of the lipid content of foods, but also includes waxes and other compounds that may interfere with digestion or palatibility. It has been hypothesized that levels of secondary plant compounds in aspen may also vary between years (Gullion 1977). Therefore, yearly fluctuations in %crude fat could be a reflection of fluctuating levels of various compounds, and may not accurately represent digestible energy from fats. Bryant and Kuropat (1980) have shown that winter forage preferences of Alaskan ruffed grouse are negatively correlated with the resin content of winter browse. These authors have also shown this to be true in Canada. Staminate buds collected from preferred quaking aspen clones in Alberta were less resinous than those collected from rejected clones. Furthermore, trembling aspen staminate buds collected from crops of Alberta ruffed grouse were less resinous than those collected at random from preferred trembling aspen clones. Resins of Populus contain several methylated flavonols that may inhibit protein digestion (Wollenweber 1973). Antimicrobial resins may be effective defenses against cecal digestors such as ruffed grouse, as digestion in the cecum is dependent upon the microbial fermentation of plant material. Ingestion of antimicrobial resins may reduce production of microbial protein, vitamins, and volatile fatty acids. Therefore, variations in levels of %crude fat content between years could be influencing the nutritional quality of flower buds as well as vegetative buds for ruffed grouse.

Aspen catkins show a wide variation in nutrient content between years. Most of the differences observed are felt to be due to the rapid progressive changes in plant physiology at the time of flowering, as flower development is highly temperature dependent. Catkin elongation and pollen shed can occur as rapidly as a few hours if temperatures are high. Genetic differences in flowering phenology between clones also influences the physiological stage of catkin development at a given time (Pregitzer and Barnes 1981). Therefore, standardization between years and clones was difficult to achieve, probably accounting for the wide variations observed.

In evaluating differences between sexes, male trembling flower buds and catkins had higher %crude fat and caloric values than female catkins and buds. In terms of total fiber, males appear to be more digestible than females, although higher levels of digestion inhibiting compounds in the %crude fat of males could potentially reduce digestibility. In terms of protein no differences existed between sexes. It appears that bud size, and therefore the amount of nutrients consumed per bite, may be the major difference between male and female flower buds. Huemphner (1981), in a study of ruffed grouse winter arboreal feeding behavior, also felt that bud size may be an important factor determining canopy and perhaps clone preference.

Studies by Huemphner (1981) have shown an approximate preference of 2:1 for trembling aspen flower buds over those of bigtooth aspen. Huemphner also found that during high ruffed grouse population densities, bigtooth aspen was utilized more heavily than during low ruffed grouse population densities. When comparing the 2 species, bigtooth flower buds were higher in %crude protein and lower in apparent digestibility than male trembling flower buds. No differences were found in %crude fat. When evaluating the nutritional quality of vegetative buds from both species, it appears that bigtooth vegetative buds are of lower nutritional quality than trembling buds, as %total fiber was higher, and %crude fat, %crude protein, and caloric value were lower.

Aspen leaves are a highly preferred late spring and summer food for ruffed grouse. At Cloquet in Minnesota, leaves ranked first among all identifible materials (Vanderschagen 1970). In this study, aspen leaves contained a significant amount of protein, the mean being higher than that of male flower buds or male catkins. It must be remembered however, that these samples were collected in early spring at the time of leaf flush, accounting for the high protein levels. Results indicate that bigtooth leaves were higher in protein, but this result is felt to be the consequence of leaf phenology at the time of sampling, as trembling aspen were about 2 weeks ahead of bigtooth leaves in terms of phenological development and therefore would be expected to have lower levels of protein. Laying and incubating female ruffed grouse feed for only short periods during the day. Therefore, they need to obtain a highly nutritious diet in a relatively short period of time. Maxon (1974), using telemetry to study female ruffed grouse in Minnesota, found that female ruffed grouse have a marked preference for trembling aspen leaves as a food source during incubation. Our data suggest that aspen leaves provide ruffed grouse with a highly nutritious and easily digestible food resource at this time of the year.

The Standard Metabolic Rate (SMR) for a 644 g ruffed grouse has been calculated to be 46.1 kcal/day, assuming a respirtatory quotient of 0.80 (Rasmussen and Brander 1973). The energy reserves of ruffed grouse may not last more than a few days, consequently regular feeding must be a vital component in the energy budget of ruffed grouse during winter. For maintenance of a long term energy balance, the daily quantity of energy metabolized from the food must at least equal the daily energy expenditure. Data indicate that staminate flower buds of both species provide a greater amount of nutrients per bud than vegetative or pistillate flower buds. This may account for the observed preference for staminate buds as the male flower buds would allow the birds to "fill up" quickly, thus reducing the time exposed to predation as well as reducing energy expended to maintain body temperature. It should also be noted though, that this study has shown an observed sex ratio that is skewed towards male trees. Previous studies of ruffed grouse food preferences have not determined the sex ratio in the sampling area. A sex ratio skewed towards males would automatically show a preference toward male trees, as the availability of male trees would be greater than the availablity of female trees.

Foods other than aspen may be extremely important to ruffed grouse when we consider the variability of aspen in terms of both bud production and nutritional quality. Gray (unpub. data), in evaluating the nutritional quality of black cherry (P. serotina), paper birch (B. papyrifera), yellow birch (B. lutea), alder (Alnus rugosa), and willow (Salix discolor) buds in the Pigeon River Country State Forest of Michigan, found that many of these species were similar or often higher in nutritional quality and energetic value than aspen. Other researchers have also shown paper birch catkins and buds (Schemnitz 1970), and black cherry buds (Bump et al. 1947), to have higher or similar levels of %crude protein and %crude fat than aspen flower buds. Studies in Minnesota have shown the winter diet of ruffed grouse to have marked variations from one year to the next (Doerr 1973; Vanderschaegen, 1970). Therefore, it is felt that although aspen appears to be an important food source to ruffed grouse, the availability of other foods in the forest composition may be an extremely important habitat component in terms of winter foraging.

Ruffed grouse have been shown to preferentially feed on certain aspen clones, although no consistent relationship has been found between the forage preferences of ruffed grouse and the phosphorous, micronutrient, soluble carbohydrate, or fiber content of trembling aspen (Doerr et al. 1974). Currently it is being speculated that yearly variations in nutritional quality and/or yearly variations in bud production may be influencing the ability of ruffed grouse to maintain the nutritional plane required to survive winter and/or breed and raise broods successfully in the spring.

Studies (Ficher 1939; Bump et al. 1947) have indicated that the abundance of ruffed grouse is not uniform throughout its range. That is, birds have been known to be increasing in some localities while decreasing in others. If ruffed grouse population fluctuations are a response to the quantity and/or quality of food resources during the time of year when food resources are scarce, yearly variation in aspen nutrition and production may influence ruffed grouse population cycles. The fact that ruffed grouse inhabit relatively limited ranges throughout their lifetime makes them subject to nutritional stresses brought about by the variant nutrient composition of materials from relatively few plant species. Therefore, the combination of low bud production, varying nutritional quality, digestion inhibiting compounds in crude fat, and the availability of foods other than aspen could trigger the population levels to oscillate over time in response to specific environmental conditions and the quality and availability of food resources.

MANAGEMENT IMPLICATIONS

Our results include a number of findings pertinent to ruffed grouse habitat management. Current habitat management recommendations suggest leaving mature male aspen clones in large aspen clearcuts to provide winter food. Our results indicate that because of the clonal growth habit of aspen, it would be disadvantageous to ruffed grouse for forest managers to leave aspen clones that are regular and/or prolific flower bud producers. That is, in terms of aspen as a ruffed grouse winter food, by leaving flowering clones standing we are in essence loosing the superior genetic stock. Ideally, to improve the genetic quality of aspen stands for ruffed grouse, managers should manipulate the clonal composition of an area to reduce the proportion of inferior clones, thereby perpetuating and expanding prolific and/or regular flower bud producers. Furthermore, the current recommendation of leaving only male aspen may also be questioned. The nutritional data from this study suggest that nutritional differences between sexes are not highly significant, especially in terms of %crude protein and %crude fat, the nutritional components that may be physiologically the most important to ruffed grouse during winter and early spring. Highly productive female clones may therefore also contribute an important food resource.

Yearly variations in aspen flower bud production appears to be a function of environmental factors and/or genetics. Therefore, yearly fluctuations cannot be managed for specifically at this time. One management suggestion is to leave enough mature aspen so that there is adequate food even during years of low bud production.

Furthermore, and perhaps most importantly, it is feel that further research on aspen as a winter food resource is needed. Further evaluation of yearly bud production and the types and levels of compounds in crude fat are needed. It is also felt that yearly production and nutritional information for "other" ruffed grouse winter foods is needed. And finally, to bring the research full circle, a complete knowledge of the energetic and nutritional requirements of ruffed grouse must be obtained to begin to understand the influence that aspen may have on ruffed grouse population cycles.

APPENDICES

Table 9. Characteristics for field identification of aspen clones by season. (from Barnes 1969)

Spring

1. Sex
2. Time of flowering and floral characteristics
3. Time, color, and progression of leaf flushing

Autumn

1. Leaf coloration
2. Time and progression of leaf fall

Summer

1. Leaf shape (BW/BL ratio), color, and size
2. Configuration of blade base
3. Leaf margin: tooth number, size, and shape
4. Configuration of blade tip

All Seasons

Bark characteristics
- 1. Bark texture
- 2. Bark color

Stem Characteristics
- 1. Stem form
- 2. Branching habit
- 3. Suceptibility to injury
- 5. Vertical profile
- 6. Miscellaneous
  - a. pruning ability
  - b. leaf rust
  - c. aphic galls

Table 10. Means, standard errors and ranges by year for nutritional components, bud weights and ages of male and female trembling aspen flower buds collected in the Pigeon River Country State Forest of Michigan.

		Male Trembling Aspen 1985(n=9) 1986(n=31)		Female Trembling Aspen 1985(n=3) 1986(n=6)	
Components	Year	Mean (S.E.)'	Range	Mean (S.E.)	Range
Bud Weight (g)	1985	0.09(0.01)	0.03-0.13	0.04(0.01)	0.03-0.04
	1986	0.13(0.02)	0.04-0.17	0.06(0.01)	0.04-0.08
% D.M.	1985	0.96(0.02)	0.94-0.96	0.96(0.03)	0.95-0.96
	1986	0.95(0.01)	0.93-0.97	0.95(0.01)	0.97-0.94
% Ash	1985	2.54(0.12)	2.09-3.15	2.65(0.19)	2.26-2.91
	1986	2.30(0.07)	1.27-3.35	2.49(0.17)	1.90-3.25
% NDF	1985	59.20(0.83)	56.04-63.52	63.00(0.78)	61.67-64.39
	1986	59.45(0.47)	53.28-64.49	64.88(1.42)	59.18-69.51
% ADF	1985	46.68(1.04)	39.88-51.88	49.70(1.96)	45.79-51.76
	1986	47.53(0.43)	42.70-49.85	52.83(1.18)	49.54-57.65
% ADL	1985	26.22(1.00)	21.40-30.42	29.99(0.69)	28.67-31.15
	1986	28.20(0.40)	23.78-33.78	30.14(0.59)	28.21-31.97
% Hemicellulose	1985	12.52(0.99)	8.28-17.37	13.30(1.34)	11.39-15.88
	1986	11.91(0.37)	6.56-17.58	12.38(1.43)	9.52-19.31
% Cellulose	1985	15.94(1.70)	17.50-25.08	19.71(2.09)	15.72-22.79
	1986	19.33(0.38)	16.75-24.29	22.40(1.24)	18.80-26.93
% Crude Fat	1985	20.06(0.74)	16.59-23.80	16.58(0.44)	16.01-17.44
	1986	14.94(0.44)	9.10-20.48	12.01(1.10)	9.52-16.36
% Crude Protein	1985	10.05(0.45)	7.56-12.06	10.88(0.26)	10.56-11.41
	1986	10.34(0.22)	8.25-13.12	9.56(0.51)	8.37-15.56
Caloric Value (Kcal/g)	1985	4.68(0.91)	4.18- 5.01	4.52(0.02)	4.51- 4.59
	1986	4.79(0.19)	4.61- 5.13	4.71(0.04)	4.52- 4.84
Age (yrs)	1985	38.66	17.00-65.00	31.00	21.00-50.00
	1986	33.48	15.00-60.00	27.57	16.00-50.00

' Standard Error

Table 11. Means, standard errors and ranges by year for nutritional components and ages of male and female trembling aspen catkins collected in the Pigeon River Country State Forest of Michigan.

		Male Trembling Aspen 1985(n=2) 1986(n=19)		Female Trembling Aspen 1985(n=3) 1986(n=8)	
Components	Year	Mean (S.E.)'	Range	Mean (S.E.)	Range
% D.M.	1985	0.94(0.01)	0.94-0.95	0.96(0.01)	0.94- 0.98
	1986	0.95(0.01)	0.93-0.97	0.96(0.01)	0.94- 0.97
% Ash	1985	4.24(0.13)	4.11- 4.30	5.80(1.30)	4.08- 8.35
	1986	4.78(0.14)	3.76- 5.96	5.70(0.45)	3.86- 7.32
% NDF	1985	54.43(3.80)	50.63-58.23	57.57(2.34)	54.18-62.05
	1986	51.01(0.75)	46.30-56.95	56.10(0.94)	53.36-60.97
% ADF	1985	42.87(1.04)	41.83-43.92	47.30(2.60)	42.28-51.01
	1986	39.86(0.65)	35.97-44.44	45.00(1.37)	39.67-51.65
% ADL	1985	23.59(1.31)	22.28-24.90	26.79(1.25)	24.48-28.78
	1986	21.03(0.49)	16.36-24.36	24.37(0.79)	20.24-26.53
% Hemicellulose	1985	11.55(2.75)	8.80-14.31	10.27(1.22)	7.83-11.90
	1986	11.15(0.44)	8.67-14.63	11.10(0.81)	8.09-14.21
% Cellulose	1985	19.28(0.25)	18.02-19.55	20.51(1.37)	17.80-22.23
	1986	18.83(0.35)	16.55-21.40	20.63(0.84)	17.24-24.89
% Crude Fat	1985	19.72(1.65)	18.07-21.37	12.94(1.05)	10.99-13.79
	1986	10.41(0.33)	8.38-13.27	9.73(0.66)	7.42-13.55
% Crude Protein	1985	11.56(1.56)	10.00-13.13	14.50(0.57)	13.75-15.63
	1986	13.51(0.54)	9.81-18.94	16.01(0.98)	12.37-21.31
Caloric Value	1985	4.41(0.15)	4.26- 4.55	4.60(0.09)	4.46- 4.77
(K cal/g)	1986	4.57(0.04)	4.29- 4.77	4.53(0.11)	4.32- 4.68
Age (yrs)	1985	33.50	17.00-50.00	35.66	18.00-50.00
	1986	32.74	15.00-60.00	24.37	20.00-45.00

'Standard Error

Table 12. Means, standard errors and ranges by year for nutritional components, bud weights and ages of trembling aspen vegetative buds and leaves collected in the Pigeon River Country State Forest of Michigan.

		Vegetative Buds 1985 (n=24) 1986 (n=18)		Leaves 1985 (n=15)	
Components	Year	Mean (S.E.)'	Range	Mean (S.E.)	Range
Bud Weight (g)	1985	0.26 (0.01)	0.01-0.04	-----	-----
	1986	0.03 (0.01)	0.02-0.04	-----	-----
% DM	1985	0.96 (0.15)	0.93- 0.97	0.95 (0.56)	0.91- 0.97
	1986	0.96 (0.01)	0.94- 0.97	-----	-----
% Ash	1985	2.57 (0.07)	1.87-3.31	5.61 (0.17)	4.12- 6.66
	1986	2.63 (0.11)	1.77-3.55	-----	-----
% NDF	1985	58.98 (1.04)	50.10-69.88	53.41 (0.66)	48.60-57.38
	1986	56.30 (1.07)	50.08-65.62	-----	-----
% ADF	1985	49.44 (0.84)	41.75-58.20	44.64 (1.02)	38.72-53.20
	1986	49.50 (0.81)	44.79-54.57	-----	-----
% ADL	1985	33.42 (0.72)	29.11-41.13	30.79 (1.03)	24.63-39.11
	1986	34.42 (0.82)	28.02-38.87	-----	-----
% Hemicellulose	1985	9.54 (0.41)	6.47-13.09	8.76 (0.53)	4.18-11.28
	1986	7.31 (0.68)	3.38-12.73	-----	-----
% Cellulose	1985	16.02 (0.49)	10.24-20.63	13.85 (0.56)	10.55-17.92
	1986	14.76 (0.50)	10.09-17.68	-----	-----
% Crude Fat	1985	23.34 (1.27)	11.23-33.48	10.85 (0.78)	6.62-17.75
	1986	18.24 (1.31)	9.69-27.69	-----	-----
% Crude Protein	1985	6.44 (0.15)	4.75- 8.19	22.05 (1.35)	15.03-32.38
	1986	8.58 (0.24)	7.12-10.31	-----	-----
Caloric Value (Kcal/g)	1985	5.15 (0.97)	4.80- 5.52	4.73 (0.05)	4.15- 4.86
	1986	5.06 (0.27)	4.68- 5.40	-----	-----
Age (yrs)	1985	38.62	17.00-64.00	35.00	16.00-61.00
	1986	31.17	18.00-50.00	-----	-----

' Standard Error

Table 13. Means, standard errors and ranges by year for nutritional components, bud weights and ages of bigtooth aspen flower buds and catkins collected in the Pigeon River Country State Forest of Michigan.

		Male Flower Buds 1985(n=7) 1986(n=7)		Male Catkins 1985(n=5) 1986(n=11)	
Components	Year	Mean (S.E.)'	Range	Mean (S.E.)	Range
Bud Weight (g)	1985	0.07(0.01)	0.05- 0.10	-----	-----
	1986	0.11(0.01)	0.08- 0.13	-----	-----
% D.M.	1985	0.96(0.36)	0.94- 0.97	0.95(0.01)	0.93- 0.96
	1986	0.96(0.01)	0.94- 0.97	0.96(0.01)	0.94- 0.98
% Ash	1985	2.89(0.08)	2.57- 3.21	5.37(0.59)	3.59- 7.21
	1986	2.79(0.15)	2.47- 3.68	5.48(0.24)	4.30- 7.08
% NDF	1985	55.67(0.16)	49.49-61.73	54.49(1.46)	50.73-59.02
	1986	55.44(0.56)	52.55-57.45	41.94(0.78)	37.47-45.93
% ADF	1985	40.93(0.96)	37.96-45.28	41.66(1.19)	39.62-46.14
	1986	42.67(0.92)	39.54-46.81	30.07(0.70)	25.35-33.57
% ADL	1985	21.65(0.59)	19.88-24.00	22.99(0.89)	20.50-25.98
	1986	23.15(0.70)	20.35-26.19	17.26(0.50)	14.10-20.49
% Hemicellulose	1985	14.74(1.06)	10.50-16.45	12.83(0.64)	10.65-14.17
	1986	12.71(0.71)	9.31-16.12	11.81(0.73)	8.64-14.39
% Cellulose	1985	19.28(0.45)	18.08-21.76	18.66(0.65)	16.54-19.61
	1986	19.26(0.32)	18.42-20.67	12.86(0.41)	11.25-16.38
% Crude Fat	1985	16.13(0.89)	12.62-19.33	12.44(1.64)	9.61-18.67
	1986	13.60(1.32)	9.29-18.57	6.48(0.35)	4.11- 8.53
% Crude Protein	1985	10.72(0.43)	9.00-12.38	16.64(1.05)	13.36-19.44
	1986	11.69(0.14)	11.12-12.37	19.03(0.55)	16.31-22.81
Caloric Value (Kcal/g)	1985	4.68(0.10)	4.18- 5.00	4.17(0.25)	3.66- 4.54
	1986	4.58(0.03)	4.41- 4.72	4.45(0.01)	4.39- 4.52
Age (yrs)	1985	51.71	35.00-64.00	46.20	35.00-50.00
	1986	49.30	40.00-60.00	53.27	40.00-64.00

' Standard Error

Table 14. Means, standard errors and ranges by year for nutritional components, bud weights and ... of bigtooth aspen vegetative buds and leaves collected in the Pigeon River Country State Forest of Michigan.

		Vegetative Buds 1985(n=18) 1986(n=7)		Leaves 1985(n=15)	
Components	Year	Mean (S.E.)	Range	Mean (S.E.)	Range
Bud Weight (g)	1985	0.03(0.01)	0.02- 0.05	——	——
	1986	0.03(0.01)	0.02- 0.04	——	——
% D.M.	1985	0.96(0.01)	0,96- 0.97	0.96(0.01)	0.93- 0.96
	1986	0.96(0.01)	0.95- 0.97	——	——
% Ash	1985	3.85(0.09)	3.08- 4.46	6.69(0.14)	6.35- 7.86
	1986	3.71(0.15)	3.19- 4.34	——	——
% NDF	1985	66.56(0.63)	62.50-70.93	52.30(0.74)	47.77-56.36
	1986	66.02(0.72)	63.37-68.10	——	——
% ADF	1985	52.40(0.49)	48.51-54.93	35.21(1.35)	27.59-46.48
	1986	52.55(0.64)	50.52-54.67	——	——
% ADL	1985	30.13(0.57)	26.50-35.29	19.75(1.66)	12.60-33.04
	1986	30.92(0.83)	30.08-34.69	——	——
% Hemicellulose	1985	14.17(0.45)	9.66-12.09	18.02(1.47)	7.69-27.98
	1986	13.72(0.39)	12.23-14.94	——	——
% Cellulose	1985	22.27(0.41)	18.63-24.90	15.44(0.53)	12.12-19.04
	1986	21.63(0.38)	19.98-22.79	——	——
% Crude Fat	1985	12.33(0.51)	9.85-19.33	11.43(0.55)	8.55-15.32
	1986	6.38(0.43)	4.88- 7.06	——	——
% Crude Protein	1985	5.90(0.21)	5.13- 8.78	25.73(0.87)	20.19-33.25
	1986	7.67(0.42)	6.31- 9.75	——	——
Caloric Value (Kcal/g)	1985	4.59(0.04)	4.24- 4.80	4.47(0.05)	4.24- 4.84
	1986	4.65(0.04)	4.51- 4.86	——	——
Age (yrs)	1985	46.44	14.00-75.00	45.46	19.00-67.00
	1986	44.85	19.00-60.00	——	——

' standard error

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