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ABUNDANCE AND PRODUCTIVITY OF BEAR FOOD SPECIES IN DIFFERENT FOREST TYPES OF NORTHCENTRAL MINNESOTA

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Abstract: Growth and reproduction of black bears (*Ursus americanus*) have been linked to food availability, particularly berries and nuts. However, quantitative data on availability of fruits in different habitats are lacking. Fruit production is highly variable and precise measurements such as berry counts are very time consuming. We used visual ratings in conjunction with systematic sampling to characterize the areal coverage and productivity of 22 species of herbs and shrubs that produce food for bears in 11 common forest types in northcentral Minnesota. We made sample counts of berries and nuts to relate visual ratings to fruit biomass. Abundance of fruit-producing species was highest in regenerating (5-15-year-old) aspen (*Populus tremuloides*) stands, but total fruit production was highest in 8-20-year-old red pine (*Pinus resinosa*) plantations that contained interspersed openings of windrowed slash. Fruit yields were poorest under dense (>80% closed) canopies and in lowland forest types, but lowlands provided a different array of species from uplands. Subjective ratings were less precise than actual berry counts but could be conducted more quickly, and they were accurate enough to distinguish important differences among stands. Because many stands could be surveyed during the short berry season, the technique enabled us to compare fruit yields across years and among different forest types, ages and canopy densities.

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Regional differences in growth and reproduction of black bears have been attributed to differences in food supply (Beecham 1980, Alt 1982, Hugie 1982). Similarly, differences in reproduction among females within a population and year-to-year differences for individual females have been linked to nutrition (Rogers 1976, 1987; Eiler 1981; Elowe 1987). However, few bear researchers have actually measured food abundance coincident with population dynamics studies. Rogers (1976) and Elowe (1987) used general observations made during field work to classify fruit and mast abundance in different years as scarce, moderately abundant, or very abundant. Though adequate for assessing gross year-to-year trends within an area, that method provided no standardized data for comparing food abundance across regions or among forest types within a region. Also relationships between food abundance and other factors such as forest density, age, and management practices could not be examined.

In recent years, forest managers have requested specific information on how to enhance habitat for bears. Many managers have been looking to habitat suitability models to aid them in making management decisions. But for forest management recommendations and habitat models to be useful, we must first define the relationships between bear reproduction, habitat composition, silvicultural practices, and food abundance. We felt it important, as part of an ongoing research project on the population dynamics of bears in northcentral Minnesota (Garshelis, D.L., K.V. Noyce, and P.L. Coy, Minn. Dep. Nat. Resour. [MNDNR], Annu. Res. Rep, 1989), to measure the abundance of bear foods, particularly berries and nuts, as they differed among forest types and fluctuated from year to year. Black bears in Minnesota eat a wide variety of foods, including large quantities of green vegetation,

ants, fruits, and nuts. However, as reported elsewhere (Alt 1980), they gain most of their summer weight on the berries and nuts eaten after mid-July (MNDNR unpubl. data). These foods appear to have the greatest influence on reproduction (Rogers 1976, Eiler 1981, Elowe 1987) and they are the most variable in abundance.

Fruit production is difficult to measure in the wild due to high temporal and spatial variability and the clumped distribution of fruit-bearing species within the mosaic of forest types. Counting and weighing fruits on sample plots is typically too time consuming to allow broad characterization of fruit availability on a forest-wide basis. Due to the sampling time required, sample sizes are usually limited and resulting variances are too high for statistical comparisons. Arimond (1979) counted and weighed fruits eaten by black bears in northeastern Minnesota but sampled few stands of each forest type. Martin (1983) measured fruit yield response to logging practices in grizzly bear habitat, but limited her work to globe huckleberry (*Vaccinium globulare*). Powell and Seaman (1990) collected and weighed fruits to determine forest-wide production from several species on the Pisgah Bear Sanctuary, North Carolina, but they did not examine differences relating to forest type, and their survey required many field personnel. We combined subjective ratings with systematic sampling to develop a sampling method that was quick and statistically repeatable. This enabled a team of 2 workers to sample a variety of forest types each summer and all the major fruit-bearing species used by bears except oak. Oak is widely scattered in the study area. Because of its high canopy, we used a different method to assess acorn production, which is not discussed in this paper.

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STUDY AREA

The study area was located in the Marcell District of the CNF and the adjoining George Washington State Forest (47°35'N, 93°37'W) in northcentral Minnesota approximately 150 km northwest of Duluth. The area is over 95% forested, with major forest types typical of the transition between the eastern hardwood and northern boreal forests. Aspen, alone or in association with white birch (*Betula papyrifera*) and balsam fir (*Abies balsamea*), predominates, with lesser amounts of red pine, maple-basswood (*Acer saccharum-Tilia americana*), and red oak (*Quercus rubrum*). Lowland forests comprise approximately 33% of the forested area (CNF and MNDNR inventory records), and include balsam poplar (*Populus balsamifera*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), northern white cedar (*Thuja occidentalis*) and black ash (*Fraxinus nigra*). Non-forested sedge meadows (*Carex* spp.), brushy lowlands, ericaceous bogs, and lakes are common. Soils are principally formed on morainic sands and sandy loams, outwash sands and silts, and organic peat. Greater than 85% of the forested land is in public ownership and is heavily managed for timber production, primarily aspen for pulp and chip products, red pine for lumber, and some spruce for pulp. Most hardwood cutting is for firewood and is often followed by conversion to aspen or pine.

METHODS

During July-August, 1984-88, we sampled 11 common forest types for the abundance and productivity of 22 fruit-bearing species eaten by bears (Table 1). We sampled 5 types in 1984 and 1985: mature aspen (>30 yrs), aspen regeneration (5-15 yrs), mature red pine (>35 yrs), young pine plantations (8-20 yrs), and mature maple (>55 yrs). Five more types were added in 1986: lowland aspen (balsam poplar mixed with aspen), black ash, white cedar, black spruce-tamarack and lowland brush (*Alnus rugosa-Salix* spp.). In 1987, we added white birch and discontinued sampling of cedar, spruce-tamarack, low-

Table 1. Herbs and shrubs that produce fruits consumed by black bears^a in northcentral Minnesota.

Scientific name	Common name
<i>Amelanchier</i> spp.	Juneberry
<i>Aralia nudicaulis</i>	Wild sarsaparilla
<i>Aralia racemosa</i>	Spikenard
<i>Cornus alternifolia</i>	Alternate-leaf dogwood
<i>Cornus rugosa</i>	Roundleaf dogwood
<i>Cornus stolonifera</i>	Red-osier dogwood
<i>Corylus cornuta</i>	Beaked hazel
<i>Prunus americana</i> and <i>P. nigra</i>	Plum
<i>Prunus pensylvanica</i>	Pincherry
<i>Prunus virginiana</i>	Chokecherry
<i>Rhamnus alnifolia</i>	Swamp buckthorn
<i>Ribes cynosbati</i>	Prickly gooseberry
<i>Ribes</i> spp.	Currant
<i>Rubus allegheniensis</i> and <i>R. pensylvanicus</i>	Blackberry
<i>Rubus strigosus</i>	Red raspberry
<i>Sambucus pubens</i>	Red-berried elder
<i>Vaccinium angustifolium</i> and <i>V. myrtilloides</i>	Blueberry
<i>Viburnum rafinesquianum</i>	Arrowwood
<i>Viburnum trilobum</i>	Highbush cranberry

^a Species were chosen based on food habits data from approximately 1,000 scats collected during 1981-1985 in the study area (Garshelis et al., MNDNR, Annu. Res. Rep., 1988).

land brush and maple stands, because of the low abundance of fruits in those forest types.

Stands of at least 3 ha, characterized by the dominant tree species in the canopy, were located from an aircraft. We sampled 10 stands of each type each year, except that only 5-6 stands of maple, cedar and ash were sampled in 1988. We visited the same stands each year, unless timber harvesting occurred, in which case a new stand was substituted for each stand cut. Because of the strong emphasis on aspen management in our study area, we wanted to characterize initial changes that occurred in the establishment of aspen stands. Thus, in addition to the 11 major forest types, we sampled 6-16 stands of very young aspen (0-5 yrs) each year from 1986-88.

Within each stand, 12 circular plots of 3-m radius (28 m²) were sampled, spaced at 50-m intervals in a rectangular grid, usually 3 plots x 4 plots. First, we visually estimated percent cover of overstory canopy above each plot, including all vegetation >2 m tall except fruit-bearing species. Second, we rated on a 0-4 scale the abundance of each fruit-bearing species in each plot,

based on its percent projected ground cover. Because these percentages could not be determined exactly, we used categories we found easy to differentiate: 0 = 0%, Tr = 0 - 1%, 1 = 1 - 5%, 2 = 5 - 33%, 3 = 33-67%; 4 = 67-100%. For determining stand means, we used the mid-point percent cover value for each category to represent ratings on plots (e.g., a plot rated 3 was considered to have 50% cover).

We used a second rating of 0-4 for fruit production of each species (fruits per unit area of cover): 0 = no fruit or almost none, 1 = below average, 2 = average, 3 = above average, 4 = bumper crop. Judgments were made relative to a subjective estimate of the average crop in a favorable site for that species. We rated productivity only if species abundance in the plot was >Tr. We used a set of reference photos and periodic cross-checking among observers to help standardize ratings. To help offset possible effects of personal bias, each stand was sampled by 2 or more observers.

To relate our subjective ratings to measurable standards we determined values for productivity ratings by counting berries on 1-m² or 0.25-m² sample plots. We located plots where 1 species covered an entire plot, rated production on the 0-4 scale, then counted all berries present. We aimed for a minimum of 10 counts for each rating for each species, but did not achieve that in some cases. Samples of 100 ripe berries were collected at various locations to obtain mean weights of ripe fruits. We could then convert our 0-4 ratings to g/m² of cover, and by multiplying these values by percent cover, could estimate fruit yield for plots sampled in forest stands. Plots were averaged to obtain stand means.

We sampled each stand once during a 6-week period from early July to mid-August each summer. By the second week of July, most fruits were set and a reasonable assessment of fruit crop could be made, even for late-ripening species. Signs of successful fruiting such as empty fruiting stalks persisted on early-bearing species until mid-August, and could be counted as fruits. After that, assessing fruit production became difficult.

We obtained the age of stands from CNF and MNDNR inventory records. Soil types were determined from soil survey maps of the U.S. Soil Conservation Service (Nyberg 1987). We combined the 22 soils represented into 7 groups based on texture and moisture characteristics: Type 1 = poorly- to moderately-drained fine sandy loams, silty loams and loamy fine sands, Type 2 = poorly-drained clay, Type 3 = very poorly-drained organic soils, Type 4 = sphagnum peat, Type 5 = excessively-drained loamy sands and loamy coarse sands, Type 6 = moderately- to well-drained fine and very fine sandy loams,

Type 7 = moderately well-drained silt loams.

We calculated mean percent cover values and productivity ratings for each stand each year to compare fruit abundance among years. We used across-year means for each stand to make comparisons among soil types, canopy densities and forest types. Due to the clumped occurrence of vegetation and extreme variability in fruit production across space and time, data were skewed towards zero and low values, and could not be normalized through transformation. We therefore used Kruskal-Wallis nonparametric ANOVA's and rank sum tests to determine significance of factor effects.

RESULTS

Plant Abundance Relative to Soils and Forest Type

Six forest types occurred primarily on well-drained soils (Fig. 1) and will be referred to as upland forest types. One of these, red pine, nearly always occurred on excessively-drained, sandy soils (14 of 15 stands). Poorly-drained soils supported 5 forest types (herein referred to as lowland types): lowland aspen on poorly-drained mineral soils and black ash, cedar, lowland brush, and spruce-tamarack on poorly-drained organic soils.

Abundance of fruiting plants, measured as the sum of percent cover ratings for all species (herein referred to as total cover), was greatest on well-drained soils, moderate

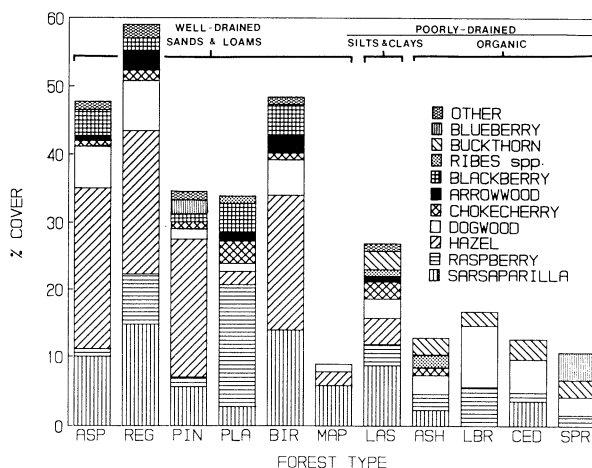


Fig. 1. Species abundance (percent cover) of fruit-bearing species in 11 forest types in northcentral Minnesota. Means for each forest type represent 2-5 years of sampling in 5-10 stands each year. For clarity, species with <0.8% cover in a forest type are not shown. "Ribes spp." represents gooseberry in uplands, currants in lowlands. "Dogwood" represents roundleaf dogwood in uplands, red-osier dogwood in lowlands. (Forest type abbreviations: ASP=aspen [>30 yrs], REG=aspen regeneration [5-15 yrs], PIN=red pine [>35 yrs], PLA=pine plantation [8-20 yrs], BIR=birch, MAP=maple, LAS=lowland aspen, ASH=black ash, LBR=lowland brush, CED=white cedar, SPR=black spruce-tamarack).

on poorly-drained mineral soils, and lowest on poorly-drained organic soils ($P < 0.05$, Fig. 1). Percent cover of sarsaparilla, hazel, and arrowwood each showed this same trend ($P < 0.05$). Consequently, these species were generally more abundant in upland forest types than in lowland types, but more abundant in lowland aspen than in other lowland types. Percent cover of blackberry, pincherry, juneberry, and wild plum was also higher on well-drained soils than on poorly-drained soils ($P < 0.05$) and roundleaf dogwood and gooseberry occurred nearly exclusively on well-drained sites. In contrast, buckthorn, highbush cranberry, currant, and red-osier dogwood almost always occurred on poorly-drained soils ($P < 0.05$) and therefore in lowland forest types.

Distribution of chokecherry and blueberry was linked more to soil texture than to soil moisture. Chokecherry was most abundant on fine-textured mineral soils ($P < 0.05$) regardless of drainage. Blueberry occurred most commonly on coarse dry soils and poorly-drained, organic soils ($P < 0.05$). Distribution of raspberry, elderberry and spikenard was independent of soil type.

Among upland forest types, the greatest total cover of fruit-bearing bear food species occurred in stands of regenerating aspen ($P < 0.01$), followed by mature aspen and birch (Fig. 1). The array of species present was similar among these 3 forest types, but raspberry was more common in aspen regeneration ($P < 0.001$), thus the total cover of fruit-bearing species was also greater. Hazel, sarsaparilla, and dogwood were the predominant fruit-producers in these 3 types. Total cover was somewhat lower in mature pine and young plantations, though still significantly higher than in maple or any lowland forest type other than lowland aspen ($P < 0.001$). Similar species occurred in mature pine as in aspen and birch, though sarsaparilla and dogwood were much less common ($P < 0.001$). Blueberry was the only species that was most abundant in mature pine ($P < 0.001$).

In contrast to mature stands, young pine plantations were dominated by raspberry, chokecherry, and blackberry and contained much smaller amounts of hazel and sarsaparilla. In plantations, occurrence of fruit-bearing shrubs was concentrated along piles of windrowed slash. Percent cover of chokecherry, raspberry, blackberry, and gooseberry was higher in plantations than in other upland types ($P < 0.01$). Sarsaparilla cover was lowest in plantations. All other species in upland forests were least abundant in maple stands.

Among lowland types, spruce-tamarack had the lowest total cover of bear food species ($P < 0.01$). Only 1 species, blueberry, was most common in these stands ($P < 0.01$). Cranberry, currant, and spikenard, though

uncommon in all types, occurred most in black ash stands ($P < 0.05$). As mentioned, sarsaparilla, hazel, and chokecherry occurred more in lowland aspen than in other lowland types. Percent cover of other species did not differ significantly among lowland types.

Diversity of fruiting species was greatest in aspen regeneration stands, which averaged 7 species with $>2\%$ cover. Lowland aspen stands had 6 such species; pine plantations, birch and black ash, 5; and mature pine and aspen stands, 4. Only 3 species averaged $>2\%$ cover in cedar and spruce-tamarack stands and 2 in maple.

Productivity Relative to Forest Type

Fruiting plants were not necessarily most productive where they were most abundant (Fig. 2). In upland stands, 5 species showed significant variation in productivity relative to forest type ($P < 0.02$). Raspberry, arrowwood and chokecherry were most productive in plantations, and secondarily in aspen regeneration. Hazel and juneberry were less productive in plantations than in aspen regeneration, pine, aspen, or birch. All these species except raspberry were least productive in maple. Productivity of sarsaparilla, dogwood, blackberry, and blueberry was not significantly related to forest type in upland sites.

In lowland stands, only sarsaparilla showed a difference in productivity among forest types. Where present, it produced the most fruit per m^2 of cover in lowland aspen, somewhat less in cedar and black ash, and almost none in spruce-tamarack and lowland brush stands ($P = 0.04$).

Effect of Overstory Canopy Density

Abundance and productivity of some fruit-bearing species were significantly related to overstory canopy density. Chokecherry, blackberry and raspberry plants were most abundant and most productive under low-density tree canopies (Fig. 3); plant abundance and productivity decreased as canopy increased ($P < 0.02$), although the productivity trend for blackberry was not significant ($P = 0.3$).

In contrast, sarsaparilla, hazel and dogwood were more abundant in stands with medium canopy densities and less abundant at low and very high densities ($P < 0.01$). Hazel also produced best under moderate canopy and dogwood produced equally well under moderate and low-density canopy ($P < 0.03$). Arrowwood and blueberry abundance showed no significant trends with canopy density. Productivity of arrowwood, sarsaparilla and blueberry appeared to be like raspberry and chokecherry,

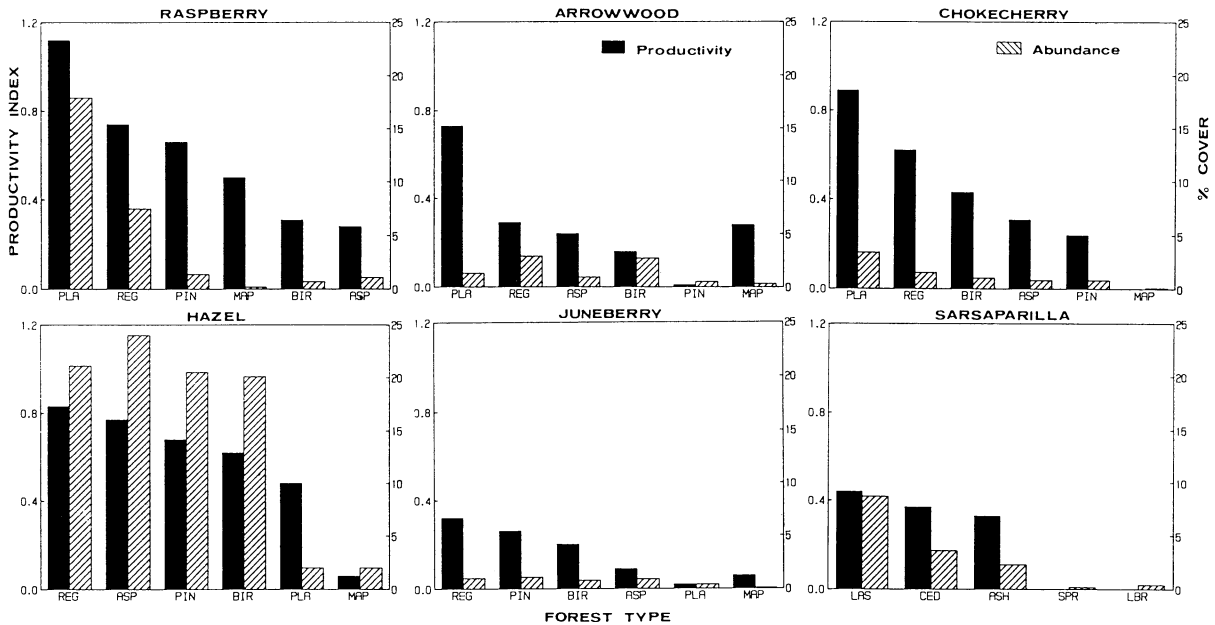


Fig. 2. Species productivity and abundance for 6 bear food species that showed significant variation in productivity in different forest types ($P < 0.05$). Upland and lowland types were tested separately; 5 species in uplands differed with forest type but only 1 in lowlands. (Forest type abbreviations: same as in Fig. 1).

with more fruit produced under less dense canopies, however, these trends were not significant ($P > 0.05$; Fig. 3). All fruits produced very poorly under high-density canopy. This corresponds to the poor fruit production observed in maple stands, all of which fell into the highest canopy density class.

Biomass Estimates for Different Species and Forest Types

Sample berry counts indicated that the numbers of fruits produced per m^2 of cover (and fruit biomass/ m^2) were very different for different bear food species, even when sample plots received the same productivity ratings (Table 2). For example, a plot of sarsaparilla rated 4 produced 215 fruits on average (43 g/m^2), whereas a plot of highbush cranberry rated 4 produced 1,211 berries (666 g/m^2). Wild plum, raspberry, blackberry, chokecherry, and highbush cranberry produced the greatest biomass of fruit per m^2 of cover: $>666 \text{ g/m}^2$ for a bumper crop rated 4, and $95\text{-}266 \text{ g/m}^2$ for a crop rated 2. In contrast, sarsaparilla and hazel produced on average only 12 and 14 g/m^2 , respectively, on plots rated 2, and 43 and 81 g/m^2 on plots rated 4. Other species were intermediate ($37\text{-}116 \text{ g/m}^2$ for rating 2, $130\text{-}485 \text{ g/m}^2$ for rating 4).

Due to the disproportionately high fruit biomass yields per m^2 of raspberry, blackberry, and chokecherry, pine

plantations surpassed other forest types in total biomass of fruit produced (Fig. 4). Forest types with understories dominated by hazel, sarsaparilla, and roundleaf dogwood produced far less total fruit biomass. Birch stands, because of the abundance and high productivity of blackberry in some locations, were second only to plantations in fruit yields. Lowland aspen, with average chokecherry production of 36 kg/ha , out-produced mature pine, maple, and all other lowland types. Maple and cedar produced negligible amounts of fruit relative to other forest types.

Year-to-Year Variation

Sizable year-to-year fluctuations in fruit production were observed for all species in all forest types. Variations in productivity ratings and biomass yields for individual species were generally similar in the major forest types where the species occurred, but trends were usually species-specific (Table 3). However, in 1985, productivity of all species except raspberry was extremely low, and in 1986 most species produced well. Raspberry in pine plantations was the most consistently high producer, except in 1988, when the crop failed due to very dry conditions. Chokecherry and blackberry, the other high producers, were much more sporadic across years in their prolificacy.

Some significant year-to-year variation also occurred

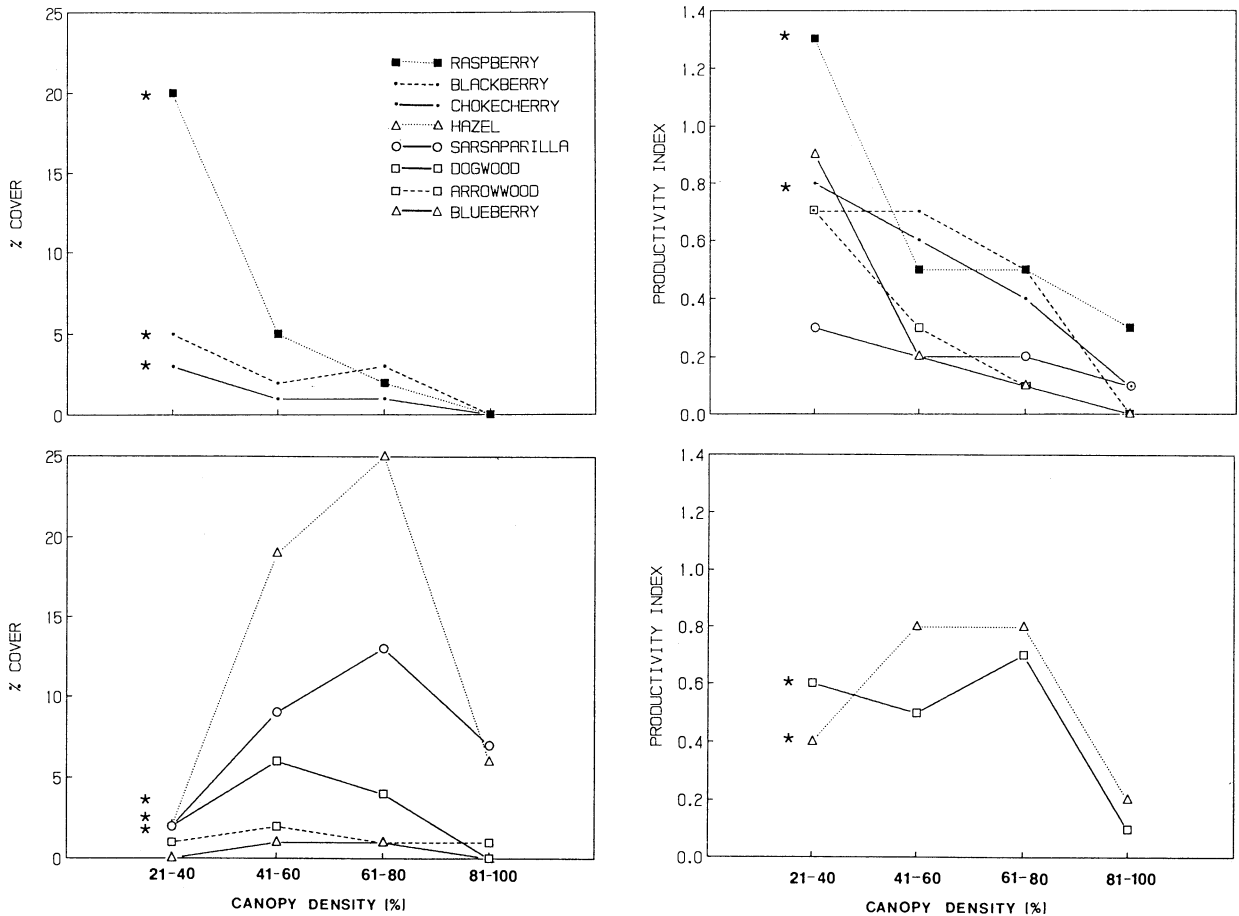


Fig. 3. Species abundance (cover) and productivity in relation to overstory canopy density for 8 bear foods in upland forest types in northcentral Minnesota. Species exhibiting significant variation with canopy class ($P < 0.05$) are marked with (*).

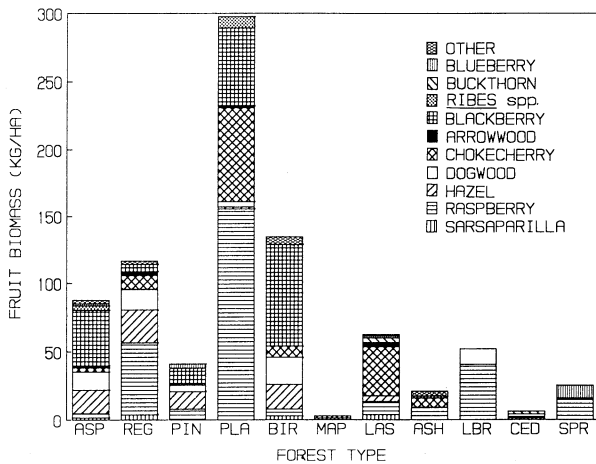


Fig. 4. Annual fruit biomass yields, calculated from percent cover and productivity ratings, of bear food species in 11 Minnesota forest types. For clarity, values < 1 kg/ha are not shown. (Forest type abbreviations and representation of "Ribes spp." and "dogwood": same as in Fig. 1).

in species abundance (Table 3). Trends did not follow productivity trends and were not always parallel in different forest types. Most species received slightly higher cover ratings in 1985 than 1984, and lower ratings again thereafter. For most species, the across-year difference did not exceed 5-6% cover, but raspberry cover in pine plantations varied from 30% in 1985 to 7% in 1988. The ubiquitousness of this trend suggested either some observer bias in 1985 or an unusual weather factor. We examined United States Department of Agriculture (USDA) weekly records of available soil moisture during May-July, 1984-88. In 1985, the mean weekly index through mid-July was 1.13, indicating much higher soil moisture than during other years of the study, when the index ranged from -0.67 to 0.67. Foliage density of perennial herbs and shrubs may reflect moisture conditions, particularly for species like raspberries that sprout many new shoots each year.

Table 2. Mean weights of fruits and yield of fruit biomass corresponding to subjective productivity ratings for 17 species.

Fruit species	Rating	Fruits per m ²	(n)	S.D.	Wt (g/100 fruits) (n)	Fruit yield (g/m ²)	Fruit species	Rating	Fruits per m ²	(n)	S.D.	Wt (g/100 fruits) (n)	Fruit yield (g/m ²)
Sarsaparilla	1	19	(24)	15.7	19.9	4	Pincherry	3	403	(4)	167.7	93	
	2	58	(17)	13.2	(15)	12		(continued)	4	1,361	(1)	-	314
	3	103	(15)	36.8		20	Highbush cranberry		1	62	(21)	45.6	55.0
	4	215	(12)	99.1		43		2	173	(14)	80.8	(22)	95
Raspberry	1	44	(30)	23.1	63.9	28	3	484	(10)	143.4		266	
	2	198	(30)	113.2	(8)	127	4	1,211	(7)	752.4		666	
	3	337	(8)	204.7		215	Gooseberry	1	10	(5)	9.6	93.7	9
	4	1,528	(8)	796.0		976		2	44	(9)	26.0	(5)	41
Blackberry	1	62	(18)	51.8	92.5	57	3	89	(4)	58.6		83	
	2	162	(20)	102.1	(14)	150	4	267	(5)	84.1		250	
	3	254	(17)	161.0		235	Spikenard	1	350	(12)	178.8	4.9	17
	4	773	(17)	344.6		715		2	750	(9)	186.9	(30)	37
Blueberry	1	113	(25)	87.3	17.0	19	3	1,158	(9)	419.5		57	
	2	512	(18)	259.3	(13)	87	4	2,659	(6)	990.4		130	
	3	1,012	(11)	298.9		172	Juneberry	1	35	(15)	33.9	41.2	14
	4	1,701	(6)	516.1		289		2	127	(8)	65.6	(7)	52
Arrowwood	1	56	(18)	49.4	21.2	12	3	180	(5)	122.8		74	
	2	216	(11)	157.0	(29)	46	4	599	(8)	401.2		247	
	3	663	(5)	265.2		141	Wild Plum	1	10	(4)	4.4	837.7	84
	4	1,254	(9)	770.0		266		2	32	(4)	12.1	(8)	268
Chokecherry	1	75	(28)	70.5	43.0	32	3	82	(5)	32.9		687	
	2	407	(16)	345.8	(47)	175	4	174	(8)	114.9		1,458	
	3	776	(11)	660.9		334	Currant	1	33	(3)	25.2	36.0	12
	4	1,930	(5)	1,128.0		830		2	200	(2)	73.5	(20)	72
Roundleaf dogwood	1	73	(21)	48.0	9.6	7	3	269	(3)	158.4		97	
	2	367	(16)	309.2	(27)	35	4	785	(2)	72.8		283	
	3	968	(15)	466.7		93	Red-osier dogwood	1	302	(5)	107.5	12.7	38
	4	2,721	(15)	845.6		261		2	915	(4)	119.7	(12)	116
Hazel	1	4	(36)	3.9	100.5	4	3	1,220	(4)	139.3		155	
	2	14	(29)	5.9	(5)	14	Buckthorn	1	22	(3)	22.9	37.0	8
	3	30	(13)	12.9		30		2	90	(0)	59.5	(4)	33
	4	81	(6)	35.2		81	3	433	(6)	203.4		160	
Pincherry	1	56	(12)	61.1	23.1	13	4	1,312	(4)	340.3		485	
	2	187	(11)	99.8	(16)	43							

Changes With Age In Aspen Stands

Abundance of fruit-bearing species differed in aspen stands of different age classes (Fig. 5). Total cover of fruiting plants averaged only 21% in stands 2-4-years-old, but 60-62% in stands 5-16-years-old. Raspberry and dogwood plants were most abundant at 5-8 years. Whereas raspberry decreased as stands matured, dogwood cover was only slightly lower in older stands. Sarsaparilla, arrowwood, chokecherry, and juneberry all were present

in greatest abundance in the 9-12 or 13-16 year age classes, and decreased somewhat in mature stands. Hazel cover was well established by 5-8 years; however, it changed little with increasing stand age. Cover of several minor species, including blueberry, plum, and spikenard, was greatest in mature and older stands.

Aspen stands 5-8-years-old produced the greatest fruit biomass. Fruits were disproportionately scarce in 0-4-year-old stands, due to the lower productivity of most

Table 3. Year-to-year fluctuations in mean productivity ratings, species abundance (cover), and fruit biomass yields for 8 bear foods in forest types common to northcentral Minnesota

Year	Sarsaparilla REG ^a		Raspberry PLA		Hazel ASP		Dogwood REG		Chokecherry PLA		Arrowwood REG		Blackberry PLA		Blueberry PIN									
	P ^b	C ^c B ^d	P	C	P	C	P	C	P	C	P	C	P	C	P	C								
1984	0.3	11	3	1.1	20	165	1.2	19	24	0.8	8	18	1.1	1	43	0.0	1	0	0.7	3	17	0.2	2	8
1985	0.1	17	<1	1.4	30	291	0.1	27	2	0.0	7	<1	0.2	4	6	0.1	2	1	0.4	6	29	0.3	4	4
1986	0.5	13	10	1.2	16	154	0.6	24	14	1.1	6	15	1.1	3	67	1.0	1	8	1.4	4	75	0.6	2	2
1987	0.1	15	2	1.0	17	130	1.0	25	27	1.1	7	35	0.8	3	12	0.3	6	2	1.3	4	140	0.0	2	0
1988	0.3	17	5	0.9	7	38	0.9	25	19	0.3	9	9	1.2	6	222	0.2	4	4	0.8	4	22	0.2	2	1

^a Ratings are given for the upland forest type where each species had the greatest coverage. Forest type abbreviations: same as in Fig. 1.

^b P = mean productivity index on 0-4 scale.

^c C = mean percent cover

^d B = fruit biomass (kg/ha).

Table 4. Mean percent cover and fruit biomass in 4 forest types in northcentral Minnesota (this study) and in northeastern Minnesota (Arimond 1979)

Forest Type ^a	Study ^b	n	Sarsaparilla			Raspberry			Blueberry			Hazel			Chokecherry		
			A ^c	\bar{x}	max ^d	A	\bar{x}	max	A	\bar{x}	max	A	\bar{x}	max	A	\bar{x}	max
REG	1	10	15	4	46	8	53	396	<1	0	0	21	24	0	2	10	157
	2	1	14	0	0	6	57	146	2	0	0	17,250	61	185	0	0	0
ASP	1	16	10	2	38	1	3	90	1	2	19	24	17	71	1	3	10
	2	4	8	17	78	<1	0	0	<1	1	6	17,791	50	546	208	0	0
PLA	1	10	3	<1	2	18	156	806	<1	0	4	2	2	39	3	70	1,386
	2	2	<1	0	0	12	858	2,090	2	47	352	8,938	0	0	0	8	22
PIN	1	17	6	1	8	1	7	117	2	3	75	21	13	66	1	1	28
	2	3	2	4	173	1	5	31	3	1	3	10,083	17	134	0	0	0

^a Forest type abbreviations: same as Fig. 1.

^b 1 = northcentral Minnesota, this study; 2 = northeastern Minnesota, Arimond (1979).

^c Species abundance, expressed as percent cover for all cases except hazel and chokecherry measured by Arimond (1979), (those expressed as stems/ha).

^d Annual fruit yield (kg/ha). Arimond's original data (dry weight) were converted to wet weight, assuming similar average weights of fresh berries from the 2 study areas.

^e Maximum annual fruit yields (kg/ha) observed in individual stands (minimum = 0 in all cases).

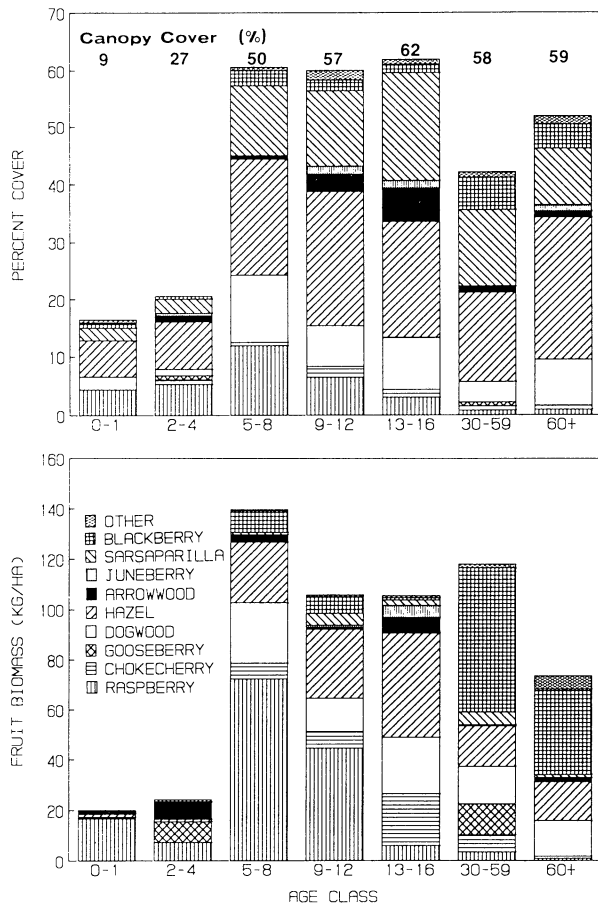


Fig. 5. Species abundance (cover) and fruit biomass yields of bear food species in aspen stands of different ages in northcentral Minnesota. Values represent means of 5-11 stands in each age class. For clarity, species abundance and fruit biomass values <0.5 are not shown.

species. Because blackberry productivity was high in 30-59-year-old stands, total fruit biomass in that age class was disproportionately high relative to total cover of fruiting plants. Sarsaparilla, though well established in 5-8-year-old stands, did not reach full production until 9-12 years. Similarly, hazel and chokecherry were present at near maximum levels by 5-8 and 2-4 years, respectively, but produced the most fruit per unit of cover in stands 13-16-years old.

The relationship between fruit abundance and tree canopy density in aspen stands was not always consistent with the relationships noted previously using all forest types. In aspen, raspberry was most abundant and most productive in stands averaging 50-57% canopy closure (Fig. 5) and chokecherry, arrowwood, and blackberry were most productive in stands with approximately 60%. In contrast, across upland forest types in general, all of these species produced best at canopy densities <40%

(Fig. 3). Fruit abundance of hazel, dogwood, and sarsaparilla decreased in older-aged stands even though percent cover of these species and overstory canopy remained fairly constant.

DISCUSSION

Occurrence and Productivity

The distribution and abundance of fruit-bearing herbs and shrubs in this study were largely consistent with what is known of species-specific requirements for optimal growth and reproduction. Most of the species we surveyed tolerate a wide range of soil conditions, but do best on light, moist, well-drained substrates, such as the sandy loams that support upland forests in our study area (Core 1974, Larson 1974, Rollins 1974, Vilkitis 1974). Hazel has narrower tolerance than some and does poorly on poorly-drained, organic, or very fine soils (Stearns 1974), such as those supporting lowland forest types. In contrast, red-osier dogwood tolerates frequent immersion of roots under water, thus is well suited to lowland forests (Smithberg 1974). Blueberry prefers acid sites like peat and acid sands (Rogers 1974). Roundleaf dogwood, arrowwood, and hazel, which we found typical of understory vegetation in mature upland forests, are reported to be well-adapted for growth under moderately dense canopy (Lesser and Wistendahl 1974, Rollins 1974, Stearns 1974). Blackberry can do well in partial shade (Core 1974), and indeed, we found it to be very productive in some mature stands, whereas pincherry and chokecherry are less shade tolerant (Fulton 1974, Vilkitis 1974).

In our study area, raspberry was the most common low shrub (greatest % cover) and sarsaparilla the most common herb that produce fruit eaten by bears. That corroborated results of previous studies in northeastern Minnesota (Arimond 1979, Ohmann and Grigal 1985). We found slightly more sarsaparilla and raspberry cover than Arimond (1979) in similar forest types, and slightly less blueberry (Table 4). Blueberry appeared to be a more important component in stands sampled by Ohmann (1984) and Ohmann and Grigal (1985), sometimes surpassing hazel in leaf and stem biomass.

Both Arimond (1979) and Ohmann (1984) found sarsaparilla plants more abundant in older pine stands than in young plantations, as we did. Dickmann et al. (1987) found that sarsaparilla increased with greater tree density in mature red pine stands of northern Michigan, whereas raspberry and blackberry were most prevalent at lower stocking rates, corroborating our findings relative to canopy density.

We cannot directly compare abundance of tall shrubs with other Minnesota studies, since Ohmann (1982, 1984) measured plant biomass, Arimond (1979) counted stem densities, and we estimated percent cover. However, in all 3 studies hazel was the dominant upland forest shrub. Roundleaf dogwood and arrowwood appeared to be less prevalent in northeastern Minnesota than in our area, occurring there primarily in mature aspen stands, rather than in regenerating aspen forests. In all 3 studies, juneberry abundance increased with stand age in aspen.

We found no references in other studies to year-to-year variation in foliage density or percent cover of perennial shrubs. We found that raspberry foliage density fluctuated significantly from year to year coincident with available spring soil moisture. This may be true of other perennial species as well.

We found few references to wild berry yields of most species included in this study. Cherkasov (1974) and Kolupaeva (1980) measured blueberry yields in Russia at 33-188 kg/ha and 160-296 kg/ha, respectively, but these were on prime berry sites. Hatler (1967) measured average yields of 220 kg/ha of blueberries in aspen and 270 kg/ha in black spruce stands of interior Alaska during a year of excellent berry production, but gave no indication of blueberry plant abundance. Our average annual blueberry yields in aspen and black spruce were much lower (2 and 9 kg/ha, respectively), however blueberry cover averaged only 1% and 4% in these types. Yields from individual spruce stands in our study ranged as high as 155 kg/ha in a given year. Though blueberry and other *Vaccinium* spp. are important to bears in northeastern Minnesota (Rogers 1976) and many other locations (Hatler 1967, Martin 1983), they rarely occur in bear scats from our study area (Garshelis, D.L., K.V. Noyce, and P.L. Coy, MNDNR, Ann. Res. Rep. 1988).

Raspberry yields of 80-1,170 kg/ha were reported from prime berry sites in Russia (Kolupaeva 1980), but again no measure of raspberry cover was given. Those yields were higher than average yields we measured for different pine plantation stands (0-333 kg/ha), but comparable to the maximum stand yield observed in this study (806 kg/ha) and to estimates of average yields (production rating 2) for areas with 100% raspberry cover (1,270 kg/ha; Table 2).

Yields of hazel measured in aspen woods of Alberta with 75% hazel cover ranged from 100-32,000 nuts/ha (Stearns 1974). Hazelnut yields in Missouri were reported at 7,400 nuts/ha (Dalke 1953). Individual aspen stands in our study area produced up to 71,000 nuts/ha (71 kg/ha), and mean production in aspen stands, which averaged 24% hazel cover, was 17,000 nuts/ha (17 kg/ha).

In the most comparable study, Arimond (1979) measured fruit yields of 5 bear foods in different forest types in northeastern Minnesota for 4 consecutive years. Mean yields of sarsaparilla, raspberry, blueberry, and hazel in the most productive forest types she sampled were much higher than means for similar forest types in our study area (Table 4). Values for less productive types were similar. Ranges in fruit yields observed were also much greater (i.e., highest yields were much higher) in Arimond's study area. Only chokecherry produced more fruit in our study area due in part to the wider distribution of chokecherry shrubs.

Reasons for these discrepancies are unclear; if they resulted solely from Arimond's small sample size for each forest type, one would expect to see greater ranges in biomass production in our larger data set. More likely, they reflected real differences between stands sampled in the 2 areas those years.

Use of Ratings

Use of subjective ratings to classify abundance and production enabled us to sample and characterize a large number of forest stands during Minnesota's short berry season. We were able to sample enough stands to make statistical comparisons among forest types, soil types, canopy closure, stand age, and year. Subjective ratings were quick to assign, yet were sensitive to major differences in fruit production and species cover from one plot to another.

We found that it was easier for observers to distinguish and categorize differences in species abundance and productivity where abundance and production were low, as opposed to where they were high (e.g., it was easier to distinguish between 10% and 20% cover than between 70% and 80% cover). Thus, categories used to classify species abundance did not represent equal divisions from 0-100%. Rather, the range of values in the lowest categories was much smaller than in the highest category (e.g., cover rating 1 = 1-5%, whereas rating 4 = 67-100%). Ratings of fruit production were similarly skewed; generally the number of fruits represented by a productivity rating increased by a factor of 2 or 3 with each consecutive rating. Consequently, ratings perhaps over-emphasized some differences among stands with low abundance and productivity - differences that were of little consequence to bears. But because there were such large differences between low- and high-producing stands, and these were the differences likely to affect bears, we felt ratings were sensitive enough to yield useful information.

Productivity ratings are subjective and species spe-

cific, thus results from studies in different areas should not be compared without first converting ratings to biomass estimates. Furthermore, it must be recognized that biomass estimates arrived at this way are based on calibrations of productivity ratings with large variances, and may not be as accurate as estimates arrived at by actually measuring production on randomly or systematically located sample plots, such as described by Powell and Seaman (1990).

Forest Management Implications

In terms of total fruit biomass and diversity of fruits produced, the most important forest types in this study were stands of 10-20-year-old red pine and 9-16-year-old regenerating aspen. Pine plantations, as managed on the Chippewa National Forest, typically consisted of blocks of 20-40 rows of pines planted between windrows of bulldozed slash. These windrows provided strips of open canopy for many years. Most fruit, particularly raspberries, occurred along or adjacent to these windrows.

Very young aspen stands (0-5 years), despite their lack of overstory canopy, did not produce the abundance of fruits found in similarly open plantations. Most likely this was because sun-loving species, such as raspberry, chokecherry, blackberry and arrowwood, were not abundant in the mature aspen stands that preceded aspen regeneration, and they did not have time to become established. The aggressive growth of aspen and consequent canopy closure from 5-15 years probably prevented those species from ever becoming as well-established or producing as well as in plantations. Instead, more shade-tolerant species such as sarsaparilla, dogwood, and hazel became the major fruit producers when aspen stands reached 9+-years-old. These species decreased somewhat in abundance and productivity as the stands matured.

Relatively low abundance of sarsaparilla, hazel, and dogwood in pine plantations, as compared to aspen regeneration stands of similar age, was probably a result of chemical treatments used in establishing young pine stands. Ohmann (1984) found that hazel was as abundant in non-chemically treated pine plantations in northeastern Minnesota as it was in aspen regeneration, whereas it was nearly absent in treated plantations. Most plantations in our study area received chemical treatment when established and some received subsequent chemical release treatments. Because of hazel's extreme sprouting vigor after disturbance (Buckman 1964, Stearns 1974), it has been specifically targeted for eradication with mechanical and chemical treatments in management of young pine plantations. Other species such as choke-

cherry, blueberry, arrowwood and juneberry, though not as competitive with young pine, nevertheless suffer from the same treatments (Arimond 1979, Ohmann 1984, MNDNR unpubl. data). Once eradicated, hazel and other shrubs can be slow to recolonize areas and produce fruit. New stems of hazel take 10 years to reach full production (Stearns 1974).

Pine plantations are an example of how relatively minor differences in forest stand management, in this case for red pine, can either enhance or virtually destroy some resource of value to wildlife. Many plantations in Minnesota and across the northcentral states are planted for maximum densities of young trees and are kept virtually devoid of fruit-bearing herbs and shrubs, first by herbicides and later by the dense pine canopy that develops. Even without herbicides, fruit-bearing shrubs in a new stand take time to recover from mechanical disturbance during previous logging. Kardell (1980) found that blueberry plant coverage and productivity decreased after logging and were adversely affected for 10 years or more, even though blueberry vigor is generally best in the open (Hoefs and Shay 1980). When plantations are managed with interspersed openings (such as along windrows), fruit-producing species in these areas can be allowed to recover and can be spared the subsequent mechanical and chemical treatments applied to the planted areas. These openings are conducive to good fruit production because of their lack of canopy and can become extremely productive patches scattered throughout the forest.

Bears rely heavily on such concentrated sources of food, whether natural or manmade. Seasonal movements to dumps, oak stands, pine nut stands, agricultural fields, and productive berry patches are widely reported (Hatler 1967; Amstrup and Beecham 1976; Garshelis 1978; Kendall 1983; Elowe 1987; Garshelis et al., MNDNR Ann. Res. Rep., 1989). Areas of concentrated food need not be large to attract bears. We have observed small concentrations of bears around particularly productive forest stands. Individual bears sometimes restrict movements around a single food source for days or weeks. When "hot spots" of bear food production can be identified (e.g., small non-commercial oak stands, scattered wild plum clusters, particularly productive plantations), forest managers can plan around them, often with little impact on goals for timber production or other forest uses. One stand of a particular type may be far more productive than most stands. Of 10 birch stands we sampled, 1 produced on average 520 kg fruit/ha and another 347 kg/ha, whereas all others produced less than 200 kg/ha and 4 of those <60 kg/ha. If forest inventory procedures can

incorporate simple schemes to rate abundance and productivity of shrub and herb species, individual stands with particular value to wildlife can be identified and preserved.

It is important to recognize that fruit biomass alone does not determine the relative importance of different forest types as foraging areas for bears. Different foods have different nutritional value and bears undoubtedly prefer some species over others. Raspberry, though overwhelmingly the most abundant fruit in our study area, occurred in bear scats less frequently than sarsaparilla (Garshelis et al., MNDNR Annu. Res. Rep., 1988). Though fruit yields in lowland forest types were low, those stands provided the major sources of red-osier dogwood and buckthorn, which regularly appeared in scats. Mature aspen and pine produced far less fruit than plantations but were major sources of sarsaparilla, wild plum and spikenard. Sarsaparilla was the single most common fruit found in bear scats during 5 years of collection, and plum and spikenard also occurred regularly. A diverse forest provides a diverse food base for bears. This helps to ensure supplies of alternate foods in years when major food species are scarce, and thus may help prevent excessive bear nuisance activity. Some forest types produce little food for bears but provide other resources, such as escape cover and den sites.

The forests of northern Minnesota support local bear populations with large differences in reproductive potential. Within our study area, there is a marked contrast between the smaller, slower maturing bears that live in areas dominated by lowland forests and the larger, early maturing residents of areas dominated by upland forests (MNDNR unpubl. data). Statewide, ages of bears harvested from 1980-1989 indicate that reproduction is synchronous in northern parts of Minnesota's bear range (presumably synchronized by periodic food shortages) and asynchronous to the south (Noyce, K. V., MNDNR, Ann. Bear Food Rep., 1988). Apparently food supply in Minnesota's forests is below the threshold that would ensure consistent and maximum reproduction of bears. Human manipulation of habitat can directly influence bear population dynamics in this type of environment by altering food diversity, abundance, and distribution.

Habitat assessment models, such as the recently developed bear habitat suitability indices (HSI's) for the northern Great Lakes region (Rogers and Allen 1987) and the coniferous-deciduous forests of New England (McLaughlin et al. 1987) attempt to predict reproductive potential of bear populations from habitat composition. Such models depend on knowing what resources bears need, where they occur, and how variations in their

availability affect reproduction and survival. Little data are available to quantify these relationships. Data on forest-wide fruit production may help us discover what levels of food abundance represent reproductive thresholds and may help us more accurately assign numeric values to habitat components included in HSI's. We are continuing work to characterize fruit abundance in different habitat components such as forest edges and stands managed with different silvicultural practices.

Fruit production data per se are not necessary for documenting relationships between reproductive performance of bears and the different habitat mosaics they inhabit. However, understanding fruit production can shed light on why the relationships are what they are, and can help in predicting what effects changes in a forest mosaic might have on bear reproduction. Powell and Seaman (1990) note that temporal and spatial variability in food abundance may have more influence on reproduction and social behavior than average food abundance. Assessing fruit production over time and space is the only way to examine this factor of variability.

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