MOOSE HABITAT AND FOREST SUCCESSION ON THE TANANA RIVER FLOODPLAIN AND YUKON-TANANA UPLAND

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Abstract: Production, availability, and utilization of woody browse by moose in winter were recorded in stands of 16 different ages on the Tanana River floodplain and the Yukon-Tanana uplands of Alaska. These stands represented primary and secondary succession following fire, flooding, and clearing. The forage available included 198 kg/ha in a 1-year-old aspen stand, 167 kg/ha in an 11-year-old birch stand, and 66 kg/ha in a 16-year-old willow stand. Stands greater than 25 years post-disturbance had less than 10 kg of browse per hectare. Aspen stands provide the most browse 1-5 years post-disturbance, whereas birch and willow stands provide the most browse between 10 and 16 years. Browsing intensities ranged from 0% to 56% in most stands, suggesting moose are below their habitat carrying capacities. The use of browse availability and consumption rates to determine carrying capacities and moose-days of use are discussed.

During winter, moose (*Alces alces*) in Alaska feed primarily on shoots and branches of willows (*Salix* spp.), paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), and cottonwood

(*P. trichocarpa*) (LeResche and Davis 1973, Cushwa and Coady 1976, Wolff 1978). These hardwoods are frequently associated with plant communities characteristic of early seral stages (LeResche et al. 1974, Viereck 1973). Browse production in early seral stage development is high, and the shoots and branches of woody browse species are numerous and within reach of browsing mammals. Trees and woody shrubs often grow out of reach in later successional stages, and thus the number of twigs available is reduced (LeResche et al. 1974, Spencer and Hakala 1964). In the Tanana region these early seral-stage plant communities are created by deposition of sand bars resulting from floodplain processes, by wildfire, and to a lesser extent by logging or other man made disturbances. The predominant climax plant communities in the taiga of interior Alaska are either white or black spruce (*Picea glauca, P. mariana*).

Forest succession and rate of change are determined by a host of factors. Among these are species composition of the disturbed community, nature of disturbance, site conditions, and availability of seeds and other reproductive materials. These factors, acting in concert, produce three basic successional patterns (Lutz 1956, Viereck 1975). The first is termed autosuccession, that is, a disturbance in black spruce, white spruce, birch or aspen results in the return of the same species in relatively pure stands. Willow, alder and other shrubs are common in the early stages of this successional pattern. Second, a disturbance in white spruce results in regeneration of birch from seed or stump sprouts and/or aspen primarily from root suckers followed by white spruce. The 1- to 20-year-old aspen and birch stands are highly productive and have been well documented as providing prime moose winter range (Spencer and Hakala 1964). The third pattern is characteristic of the floodplains of Alaska's rivers, wherein willow or willow-alder stands are replaced by poplar and white spruce. Patterns 1 and 2 are secondary succession and pattern 3 is primary succession. For variations in these patterns see Viereck (1975).

The major objective of this study was to compare browse porduction in different age communities following different types of disturbances to determine the capacity for providing moose winter range. These observations were made on the Tanana River floodplain and the adjacent Yukon-Tanana uplands.

STUDY AREAS

Table 1 presents general site and vegetation data for the areas included in this study. A further brief description of each follows:

Uplands

Wickersham (W). The Wickersham fire occurred in 1971 and covered about 6 000 ha. Wickersham-1 (W-1) is located in an area which was classified as a heavily burned, black spruce stand. Site W-3 is located in a large, unburned black spruce stand across the fire line from W-1 and is representative of the conditions in W-1 prior to the fire. Wickersham-2 (W-2) is an aspen stand burned at the same time as W-1 (willow) and located several kilometers from W-1. Wickersham-4 (W-4), the most severely disturbed site, was cleared for homesteading. Stands adjacent to the clearing are similar to WC-3. During the clearing, mineral soil was exposed placing the succession on this site somewhere between primary and secondary.

Murphy Dome (MD). Murphy Dome 1 and 2 (MD-1, MD-2) are located in a 2 000 ha area burned in 1958.

Goldstream (GS). This area burned in 1966.

Table 1. Vegetation type and description of study sites.

Site	Vegetation type	Soil type	Slope position	Elevation	Aspect	Slope %	Drainage class	Type of disturbance	Year of disturbance	Stand age when sampled	Type of succession
Uplands											
Wickersham-1	closed conifer, black spruce	Fairplay silt-loam	ridgetop	468	NNW	05	well	fire	1971	3,4,5 6,7	secondary
Wickerhsam-2	closed deciduous aspen	Not available	middle	618	SSW	15	well	fire	1971	1,4,7	secondary
Wickersham-3	closed conifer, black spruce	Fairplay silt-loam	ridgetop	468	--	0	well	fire	1900	75,76 77,78	secondary
Wickersham-4	closed conifer, black spruce	Fairplay silt-loam	middle	450	S	10-15	well	homestead clearing	1967	11	secondary
Elliot Highway	closed deciduous, paper birch	Not available	middle		SE	20	well	fire	1927	50	secondary
Goldstream	closed conifer, black spruce	Minto silt-loam	bottom	110	N	2-5	moderate	fire	1966	11	secondary
Murphy Dome-1	closed mixed, white spruce-paper birch	Not available	bottom	770	--	0	moderate	fire	1958	16,19	secondary
Murphy Dome-2	closed mixed, white spruce-paper birch	Not available	lower	770	SE	8-10	well	fire	1958	19	secondary

Table 1. Vegetation type and description of study sites--Continued.

Site	Vegetation type	Soil type	Slope position	Elevation	Aspect	Slope %	Drainage class	Type of disturbance	Year of disturbance	Stand age when sampled	Type of succession
Uplands											
Parks Highway-1	closed deciduous, aspen	Fairbanks silt loam	middle	310	W	8-10	well	fire	1942	35	secondary
Parks Highway-2	closed deciduous, aspen	Fairbanks silt loam	middle	110	S	10-15	well	fire	1927	60	secondary
Bonanza Creek	closed mixed, paper birch-white spruce-aspen	Fairbanks silt loam	middle	240	SW	8-10	well	harvest	1976	1	secondary
Floodplain											
Tanana River-1	open willow	alluvial land	--	130	--	0	well	N/A	N/A	8,9,10	primary
Tanana River-2	alder-poplar	alluvial land	--	130	--	0	well	N/A	N/A	25	primary
Tanana River-3	closed willow	alluvial land	--	130	--	0	well	N/A	N/A	16,19	primary
Tanana River-4	closed mixed, balsam poplar-white spruce	Salchaket very fine sandy loam	--	130	--	0	well	N/A	N/A	80	primary

Parks Highway (P) and Elliott Highway (E). These stands are representative of sapling- and pole-sized hardwood stands which cover large areas of the Yukon-Tanana upland and were burned 30-50 years ago.

Bonanza Creek (BC). This site was a mature upland forest harvested in 1977. Stem density of the trees prior to harvesting was 323 birch, 132 white spruce, and 43 aspen per hectare.

Floodplains

Tanana River (TR). Tanana River-1,-2,-3, and -4 represent several stages of primary successional sequence on floodplains.

METHODS

The amounts of browse available to moose and their browsing intensities were measured in May of each year after snowmelt. One 10-ha plot was established in each stand, except the Bonanza Creek area which was only 1 ha. Each plot was considered representative of the stand. The densities of trees and shrubs were determined by the point-center-quarter method (Cottam and Curtis 1956) using 40 points. Four trees or shrubs (160 per site) were sampled at each point, and the number of browsed and unbrowsed twigs on each plant recorded. A shrub consisted of single or multiple stems arising from a single base. A twig was a single branch less than 4 mm in diameter, usually a portion of the current annual growth. The Shafer (1963) twig-count method was used to estimate the availability and utilization of hardwood browse. This procedure was similar to that of Joyal (1976). The mean diameter at point of browsing was determined by measuring the diameter of 25 randomly selected browsed branches of each species. Twenty-five unbrowsed twigs of the same diameter were clipped, ovendried, and weighed in order to determine the mean weight per twig. The weight per twig was multiplied by the number of twigs per shrub and number of shrubs per hectare to provide an estimate of the total biomass of hardwood browse available to moose per hectare. The mean diameters at point of browsing (dpb) and weights per twig (Table 2) were used to compute the amount of browse available per shrub and per hectare. An estimate of browse consumed per hectare was obtained by multiplying the total browse available by the percentage of browsed twigs. Estimates of available browse included growth less than 4 mm in diameter between 50 cm and 3.5 m above the ground.

Table 2. The Diameters at Point of Browsing and Twig Weights of the Browse Plant Species Sampled.

Browse species	Diameter at point of browsing mm, (1 S.E.)	Twig Wt. g, (1 S.E.)
Scouler willow	3.6 (.02)	1.02 (.01)
Feltleaf willow	3.8 (.04)	0.84 (.02)
Sandbar willow	2.8 (.04)	0.56 (.03)
Balsam poplar	4.1 (.07)	1.32 (.07)
Cottonwood	6.0 (.14)	2.36 (.24)
Birch	3.1 (.04)	1.02 (.04)
Aspen	3.1 (.04)	0.97 (.03)
Alder	2.9 (.03)	0.68 (.04)
Highbush cranberry	3.0 (.03)	0.32 (.10)
Willows*	3.0 (.06)	0.63 (.07)

*Willows include Park willow, tall blueberry willow, Bebb willow, diamondleaf willow, and grayleaf willow.

Preference indices (P.I.) were determined for stands that had two or more browse plant species to see if moose were selecting certain plant species to the exclusion of others. The index is defined as P_{ib}/P_{is}, where

P_{ib} is the proportion of the ith species in the diet, and P_{is} is the proportion of that species in the stand. Preference indices were computed using three sets of data: number of stems, number of twigs, and biomass. These computations gave somewhat different results due to the large difference in number of twigs per stem and weights per twig.

RESULTS

Production of Available Browse

Tree and shrub densities and production of available browse are shown in Figure 1 and Table 3. These results are presented below and organized by stand type.

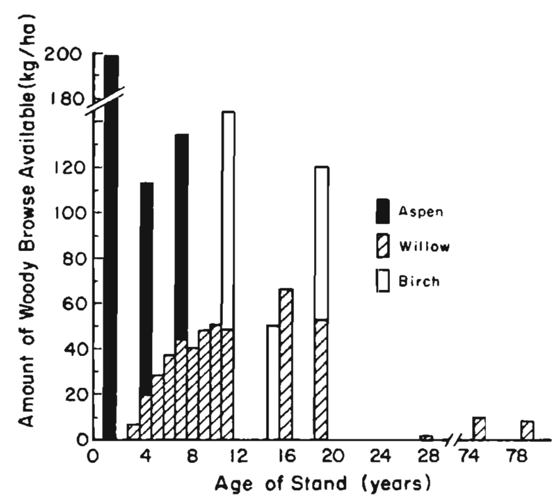

Figure 1. Amounts of woody browse available by species in stands of different age classes.

Table 3. Availability, Utilization and Browse Preferences by Species for Upland and Flood Plain Sites in the Tanana River Drainage.

Site	Age	Species	Shrubs/ ha (1 S.E.)	Twigs/ shrub (1 S.E.)	Forage available/ Shrub, g	Forage available/ ha, kg	Browse consumed ha, kg	Browsing intensity %	Frequency of occurrence	Preference index as determined by no. of: stems	twigs	biomass
Wickersham-1	+3	Scouler willow	400(13.4)	16.0(4.2)	16.3	6.5	2.9	44	74	-	-	-
	+4	Scouler willow	452(14.1)	42.0(3.7)	42.8	19.3	8.7	45	77	-	-	-
	+5	Scouler willow	638(15.0)	43.8(3.8)	44.7	28.5	7.4	26	67	-	-	-
	+6	Scouler willow	638(15.0)	57.0(3.1)	58.1	37.1	0	0	0	-	-	-
	+7	Scouler willow	638(15.0)	67.7(3.9)	69.1	44.1	8.4	19	67	-	-	-
Wickersham-2	+1	Aspen	198,375	1.0(0.0)	1.0	198.4	198.4	100(hares)	100	-	-	-
	+4	Aspen	28,945	4.0(0.2)	3.9	112.9	21.5	19	43	-	-	-
	+7	Aspen	21,645(2,769)	6.4(0.5)	6.2	134.2	0	0	0	-	-	-
Wickersham-3	+75	Scouler willow	489(16.2)	19.0(2.7)	19.4	9.5	3.2	34	53	-	-	-
	+76	Scouler willow	489(16.2)	19.0(2.7)	19.4	9.5	0.8	8	16	-	-	-
	+77	Scouler willow	489(16.2)	17.1(1.9)	17.4	8.5	0	0	0	-	-	-
	+78	Scouler willow	489(16.2)	13.2(0.8)	13.5	6.6	0	0	0	-	-	-
	+79	Scouler willow	489(16.2)	16.7(1.2)	17.0	8.3	0.8	1	9	-	-	-
Wickersham-4	+11[1]	Birch	7,645	19.7	20.1	153.7	33.8	22	63	1.0	.09	1.0
		Scouler willow	1,330	7.4	7.5	10.0	7.9	79	91	1.3	3.2	3.2
		Alder	1,330	31.2(3.0)	30.3	40.3	1.6	4	27	0.3	0.2	0.2
		Aspen	760	4.5(1.2)	4.4	3.3	1.5	44	66	2.0	7.0	2.0
			11,065(1,065)			207.3	44.8	x̄=22				
Murphy Dome-1												
	+16	Willow	10,957	3.3(0.3)	3.4	37.3	5.2	14	28	1.1	1.7	1.7
		Birch	1,895	14.8(2.1)	15.1	28.6	0.3	1	6	0.4	0.4	0.1
		Spruce	2,300	0	0	0	0	0	0			
			15,152(1,969)			65.9	5.5	x̄=8				

Table 3. Availability, Utilization and Browse Preferences by Species for Upland and Flood Plain Sites in the Tanana River Drainage --Continued.

Site	Age	Species	Shrubs/ ha (1 S.E.)	Twigs/ shrub (1 S.E.)	Forage available/ Shrub, g	Forage available/ ha, kg	Browse consumed ha, kg	Browsing intensity %	Frequency of occurrence	Preference index as determined by no. of: stems	twigs	biomass
Murphy Dome-1	+19	Willow	11,110	4.9(0.6)	4.1	45.5	15.5	34	54	1.2	1.0	1.1
		Birch	2,037	3.3(0.7)	3.4	6.9	0	0	0	0	0	0
		Alder	2,037	5.6(0.9)	3.8	7.7	0	0	0	0	0	0
		White spruce	3,334	0	0	0	0	0	0	0	0	0
			18,518			60.1	15.5	x̄=26				
Murphy Dome-2	+19	Birch	5,000	18.3(3.5)	18.7	93.5	4.7	5	13	1.5	0.9	0.8
		Willow	6,719	4.7(0.6)	3.9	26.2	2.6	10	20	0.6	1.4	1.6
		White spruce	3,906	0	0	0	0	0	0			
			15,625(1,241)			119.7	7.3	x̄=6				
Goldstream	+11	Willow	11,757	3.3(0.3)	2.8	32.9	0	0	0	-	-	-
		Birch	396	3.0(1.5)	3.1	1.2	0	0	0	-	-	-
		Balsam poplar	1,057	1.3(0.6)	1.7	1.8	0	0	0	-	-	-
			13,210(962)			35.9						
Elliot Highway	+50	Birch	4,714	0	0	0	0	0	0	-	-	-
		Alder	1,852	0	0	0	0	0	0	-	-	-
		White spruce	1,852	0	0	0	0	0	0	-	-	-
			8,418(1,007)									
Parks Highway-1		Aspen	6,618	0	0	0	0	0	0	-	-	-
	+35	Alder	216	0	0	0	0	0	0	-	-	-
		White spruce	360	0	0	0	0	0	0	-	-	-
			7,194									
Parks Highway-2		Aspen	1,392(146)	0	0	0	0	0	0	-	-	-
	+50	Aspen	11,820(1,392)	1.0(0.0)	1.0	11.8	9.1	77	77	0.7	0.9	0.9
Bonanza Creek	+1	Birch	107(16)	39.4(3.4)	40.2	4.3	3.9	91	95	1.2	1.2	1.1
			11,927			16.1	13.0	x̄=81				

Table 3. Availability, Utilization and Browse Preferences by Species for Upland and Flood Plain Sites in the Tanana River Drainage --Continued.

Site	Age	Species	Shrubs/ ha (1 S.E.)	Twigs/ shrub (1 S.E.)	Forage available/ Shrub, g	Forage available/ ha, kg	Browse consumed ha, kg	Browsing intensity %	Frequency of occurrence	Preference index as determined by no. of: stems	twigs	biomass
Tanana River-1												
	+8	Feltleaf Willow	8,286	3.8(0.5)	3.2	26.5	14.6	55	64	1.1	1.0	1.0
		Sandbar willow	3,371	3.7(0.5)	2.1	7.1	4.0	57	67	0.8	0.7	1.0
		Balsam poplar	2,388	2.0(0.2)	2.6	6.2	3.8	92	74	1.0	1.9	1.0
			14,045(3,075)			39.8	22.4	$\bar{x}$=56				
Tanana River-1												
	+9	Feltleaf willow	10,041	3.6(0.4)	3.0	30.1	0	0	0	-	-	-
		Sandbar willow	3,814	3.5(0.4)	2.0	7.6	0	0	0	-	-	-
		Balsam poplar	3,107	2.4(0.3)	3.2	9.9	0	0	0	-	-	-
			16,962(2,948)			47.6	0	0				
Tanana River-1												
	+10	Feltleaf willow	9,882	3.1(0.3)	2.6	25.7	4.9	19	19	0.6	1.1	1.2
		Sandbar willow	3,414	3.4(0.4)	1.9	6.5	2.6	40	73	3.0	1.6	2.5
		Balsam poplar	4,672	2.9(0.5)	3.8	17.8	.5	3	5	0.3	0.3	0.2
			17,968(1,330)			50.0	8.0	$\bar{x}$=16				
Tanana River-1												
	+11	Feltleaf willow	11,427	3.1(6.3)	2.6	29.7	5.6	19	29	0.8	0.9	0.9
		Sandbar willow	2,770	5.0(0.7)	2.8	7.8	4.9	63	50	29	1.7	2.2
		Balsam poplar	2,770	2.9(0.8)	3.8	10.5	0	0	0	0	0	0
		Alder	346	8.3(3.8)	5.6	1.9	0	0	0			
			17,313(866)			49.9	10.5	$\bar{x}$=21				
Tanana River-2												
	+28	Balsam poplar	1,415	0	0	0	0	0	0	-	-	-
		Alder	7,642	1.2(0.2)	0.8	6.1	0	0	0	-	-	-
		Feltleaf willow	377	0.8(0.8)	0.7	0.3	0	0	0	-	-	-
			9,434(506)			6.4	0	0	0			

Table 3. Availability, Utilization and Browse Preferences by Species for Upland and Flood Plain Sites in the Tanana River Drainage --Continued.

Site	Age	Species	Shrubs/ ha (1 S.E.)	Twigs/ shrub (1 S.E.)	Forage available/ Shrub, g	Forage available/ ha, kg	Browse consumed ha, kg	Browsing intensity %	Frequency of occurrence	Preference index as determined by no. of: stems	twigs	biomass
Tanana River-3												
	+16	Feltleaf willow	30,000	2.4(0.2)	2.0	60.0	39.6	66	89	1.4	1.5	1.2
		Tall blueberry willow	27,000	2.8(0.2)	1.3	35.1	19.7	56	68	0.8	0.7	1.0
		Park willow	2,250	3.2(0.3)	1.5	3.4	0.6	18	43	0.3	0.3	0.3
		Balsam poplar	5,000	2.1(0.2)	2.8	14.0	1.8	13	18	0.4	0.5	0.3
			64,250(16,225)			112.5	61.7	$\bar{x}$=55				
Tanana River-3												
	+19	Feltleaf willow	18,182	3.5(0.3)	2.9	52.7	12.6	24	35	-	-	-
		Willows	5,289	4.1(0.7)	1.9	10.0	0.3	3	6	-	-	-
		Alder	9,587	5.4(0.5)	3.7	35.5	0.0	0	0	-	-	-
			33,058(2280)			98.2	12.9	$\bar{x}$=13				
Tanana River-4												
	+80	Balsam poplar	2,162	0	0	0	0	0	0	-	-	-
		Alder	2,378	2.6(0.7)	1.8	4.3	0	0	0	-	-	-
		White spruce	865	0	0	0	0	0	0	-	-	-
			5,405(446)			4.3	0	0				

Uplands

Wickersham: In W-1 (willow), browse production increased from 6.5 to 44.1 kg/ha, 3 to 7 years after the fire. All browse consisted exclusively of post-fire vegetative sprouts of Scouler willow. The increase in production was due to an increase in number of shrubs for the first 5 years and an increase in number of twigs per shrub for all 7 years.

Browse production in W-2 (aspen) was greatest the 1st year after fire (198 kg/ha), decreased to 113 kg/ha 4 years after fire, and increased to 134 kg/ha 7 years after the fire. The high productivity 1 year after fire was due to a large number of stems with one twig/stem, whereas at 7 years the number of stems had decreased, but the number of twigs per stem had increased to 6.4. This stand originated from root suckers.

W-3, the unburned stand of black spruce, supported 489 willow shrubs/ha. The biomass of available browse was less than 10 kg/ha for the 5-year sampling period. The number of twigs per shrub in the unburned stand varied from 13 to 19 compared to 68 twigs/shrub in the 7-year-old burn. Some of the shrubs had branches 5 m high and were out of browsing reach.

W-4 (birch clearing) had 11,065 stems/ha, 7,645 of which were birch. The mean number of twigs per birch stem was 19.7 and yielded 153.7 kg/ha of browse. Willows, aspen, and alder yielded another 53.6 kg/ha for a total of 207.3 kg/ha of browse. This stand resulted from the establishment of seedings and was the most productive of all stands sampled.

Murphy Dome: Browse production in MD-1 was 66 and 60 kg/ha, 16 and 19 years post-fire respectively. Production of willow and birch browse decreased from 66 to 52 kg/ha during the 3-year period as alder made up 8% of the woody browse in the older stand. White spruce was also becoming more predominant in the stand at 19 years attaining a density of 3,334 stems/ha

and a height of 1 to 2 meters.

At MD-2, browse production was 119.7 kg/ha. The number of willow stems per hectare was greater than birch, but the larger number of twigs per stem (18.3 for birch and 4.7 for willow) resulted in a greater production of birch browse. Alder was not present in the birch stand, but white spruce density was 3,906 stems/ha. The birch stems averaged 6 m in height; consequently, about 25% of current annual growth less than 4 mm in diameter was above browsing height and was not included in the sampling. The browse at both Murphy Dome stands resulted from seed.

Goldstream: This 11-year-old willow stand had 25.9 kg/ha of browse. The majority of this was produced by three species: grayleaf (*Salix glauca*) feltleaf, and diamond leaf willow (*S. planifolia*), none of which were identifiable to species at the time of sampling. Birch and poplar were less dense in the stand. Spruce seedlings were abundant but all were less than 30 cm tall.

Bonanza Creek: This stand had 11,820 aspen stems/ha yielding 11.8 kg/ha of browse. These stems were root suckers and were about 1 m high. Birch regeneration was from stump sprouts which averaged 39.4 twigs /stump. Birch seedlings were also present but were less than 10 cm tall. All browse sampled in this 1-year-old stand was above snowline and available to moose as forage.

Elliott Highway: This 50-year-old stand of birch, alder, and white spruce had no browse within reach. The birch had a d.b.h. of 6 to 8 cm and a height of 6 to 8 m. The canopy was closed, and there were no other browse shrubs in the understory.

Parks Highway-1: This 35-year-old aspen stand had 6,618 stems/ha; however, the mean d.b.h. was 10 cm, and the nearest twigs were 5 m from the ground. The stand had grown out of reach of browsing mammals, and there were no other woody shrubs in the understory.

Parks Highway-2: Trees in this homogeneous, 70-year-old aspen stand had a d.b.h. of 20 cm; and the dominant trees were 21 m. No twigs were within browsing range of moose, and there were no woody shrubs in the stand. White spruce was present in the understory.

Floodplain

Tanana River: Browse production at the TR-1 increased from 39.8 to 49.9 kg/ha between 8 and 11 years of age. Feltleaf willow was the most common species present with sandbar willow and balsam poplar also present. Alder was also present in the stand but did not show up in the sampling until 11 years. The number of twigs per stem varied from 2.4 to 5.0 for all browse species. The number of stems per hectare and twigs per shrub had not changed from 9 to 11 years which suggests that maximum production of browse had probably been reached. Most shrubs were 2 to 3 m tall and within browsing reach; however, about 5% of the feltleaf willows were taller than 4 m and out of browsing range.

The 28-year-old alder stand, TR-2, produced only 6.4 kg/ha of browse, 6.1 of which was alder. The alder was 4 to 5 m tall, and the poplar was 9 m tall. All poplar twigs were higher than 4 m. Alder and poplar had taken over the stand which presumably was dominated by willows in its earlier succession.

The forage available at TR-3 (willow) was 112.5 and 98.2 kg/ha at ages 16 and 19 years. The number of willow stems per hectare decreased substantially between 16 and 19 years, while the number of alders increased. This suggests that annual productivity is probably declining. The method

used for sampling the 16-year-old stand differed slightly from the method used for the 19-year-old stand. This may have resulted in an overestimate of the 16-year-old stand and may account for the large difference in available forage. The decrease in forage available was real however, as evidenced by a large number of decadent willow stems.

The formation of the Tanana River stands (primary succession) was a more complex process than those resulting from secondary succession on the upland sites. The majority of shrubs on floodplain sites are believed to be of seed origin; however, an unknown percentage are of vegetative origin. These have resulted from production of new plants from broken branches deposited and buried during periods of high water. Shrub origin of this type is similar to seed reproduction in that the plants must establish root systems. The other exception to seed origin is that sandbar willow and balsam poplar can expand vegetatively by root suckers. The point to be made is that shrubs and trees of seed origin do not have the advantages of sprouts which arise from established root systems with stored reserves.

In the 80-year-old poplar stand, TR-4, browse production was limited to 4.3 kg/ha of alder. The poplars were 20 m tall with a d.b.h. of 20-25 cm. No other woody browse was available in the understory.

Browsing Intensities and Selectivity

Uplands

Browsing intensities and preference indices are shown in Table 3.

Wickersham: Browsing intensities at W-1 (willow) ranged from 0% to 45% during the 5-year sampling period. The heaviest browsing intensity was at 4 years, the lowest, no browsing, was at 6 years. During the years in which browsing was recorded, 67% to 77% of the shrubs had been browsed to some extent. Most shrubs which were browsed had less than 50% of their available twigs clipped and rarely was 100% of the twigs on a given shrub removed. This was true for all stands sampled.

Browsing intensity in W-2 (aspen) was 100% 1 year after the fire; however, this was due entirely to snowshoe hares (*Lepus americanus*). Moose browsing intensity was 19% at 4 years and 0% at 7 years.

Browsing intensity in the unburned stand, W-3, was 34% and 8% at 75 and 76 years respectively, then decreased to 0% and 1% for the next 3 years.

Browsing intensity at W-4 (birch clearing) was 23%. A preference was shown for aspen followed by Scouler willow, birch, and alder. This was the only stand in which alder was browsed.

Murphy Dome: Browsing intensities at the MD-1, 16 and 19 years, were 8% and 26% respectively. At MD-2 browsing intensity was 6%. Preference indices showed a definite preference for willows in the birch stand. Willows consisted of Scouler and feltleaf willows which were browsed at equal intensities. When using the preference index computed by number of stems, however, a preference was shown for birch in the birch stand. The differences in results are due to a larger number of twigs per stem on birch as compared with willow.

Goldstream: No browsing by moose was recorded at the 11-year-old stand at Goldstream. Browse was plentiful in this stand and within reach, but no browsing was recorded. There was no evidence of browsing during the previous two winters.

Bonanza Creek: Browsing intensity at the logged stand was 81%. This was the highest browsing intensity recorded. A slight preference was shown for birch; however, both aspen and birch were browsed at high intensities.

No browsing by moose was recorded in the adjacent unlogged 130-year-old stand.

Tanana River: Browsing intensities at TR-1 ranged from 0% at 9 years to a maximum of 56% at 8 years. Preference indices showed sandbar willow to be a preferred species; however, feltleaf willow also had a preference index greater than 1. Poplar had a low selectivity value, and alder was not eaten. No browsing by moose was recorded in TR-2.

Browsing intensities at TR-3 were 55% and 13% at 16 and 19 years, respectively. A slight preference was shown for feltleaf willow when the stand was sampled at 16 years with tall blueberry willow, park willow, and poplar consumed to a lesser extent. Sampling was conducted before budbreak at 19 years, so tall blueberry and park willow could not be differentiated.

No browsing by moose was recorded in the 80-year-old poplar stand, TR-4.

DISCUSSION

Species Response

Production and utilization of browse is determined by the interaction of prior stand density and composition, regeneration characteristics, growth rate of browse species, site conditions, nature of disturbance, and the impact of browsing on the vegetation.

Aspen. Aspen was present in three of the upland stands. It occurs on relatively warm, permafrost-free, upland sites and is uncommon on floodplains. Because of its ability to produce root suckers following death of the parent stem, substantial amounts of browse are produced the first full growing season following disturbance. Density and distribution of stems in young aspen sucker stands is relatively uniform compared to the aggregated or clumpy nature of birch and willow stems of vegetative origin. The genetic composition of sucker stands is such that one genotype (a clone) may cover a large area. For example, clone sizes up to 40 ha have been reported in North America (Kemperman and Barnes 1976). In the other major browse species, each stem or multi-stemmed group is genetically different. These genetic patterns could have significance with regard to selection and palatability of browse. Aspen seed reproduction is common in this region, but pure stands resulting from seed are not known.

The Wickersham aspen stand (W-3) exhibited the classic response to fire. The browse available at the end of the first growing season was the greatest observed in this study. By age 7, stem density was reduced to about 10% of that at age 1, while available browse declined to only 68%. Maintenance of browse availability at higher levels is the result of the formation of lateral branches in older stems due to browsing effects. Few, if any, lateral branches are produced by 1-year-old aspen suckers. The age at which browse is no longer available depends on site quality and other variables. Observations made in 17- and 15-year-old aspen stands indicated that the lowest branches were 2 m from the ground and 75 percent of the current annual shoot growth was over 4 m above the ground. The 35- and 60-year-old aspen stands produced no available aspen browse.

In the severely disturbed homestead clearing, W-4, aspen occurred as widely spaced single stems suggesting that they were of seed origin. Observations made in this study do not allow a comparison between browse production in seedling and sucker stands, however, our observations elsewhere in this region suggest that seedling growth is much slower than sucker growth and that 3 to 5 years or more are required before seedlings are tall

enough to provide winter browse. The result of slower growth would be to offset the productive period by this number of years. Relative rates of browse production by seed and vegetative growth are summarized in Fig. 2.

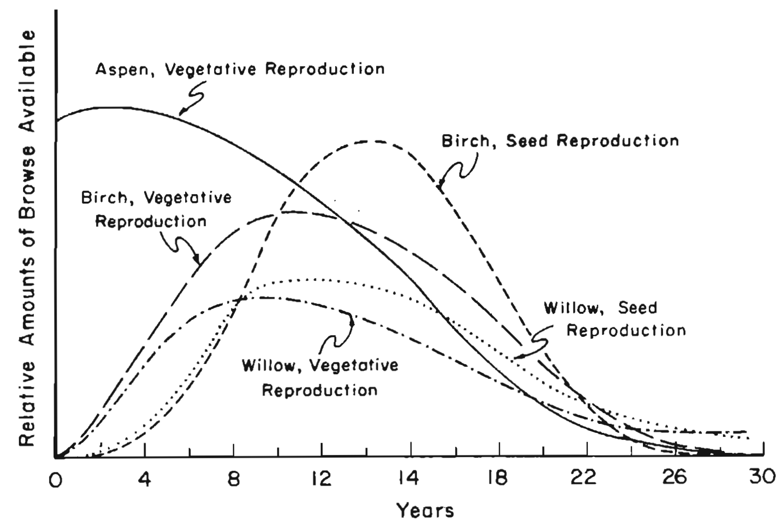

Figure 2. Rates and relative amounts of browse produced by aspen, willows, and birch by seed and vegetative growth in different aged stands.

Birch: Birch, which occurs primarily on upland sites, was a major component in six of the stands examined. It is also found to a limited extent in older successional floodplain stands. Birch has a wider tolerance than aspen in that it occurs on the same sites plus somewhat colder sites (Gregory and Haack 1965).

Regeneration of birch occurs from seed and stump sprouts. Stems resulting from vegetative reproduction of birch are fast growing and produce moose browse at the end of the first full growing season (e.g.

stand BC, Table 3 and Fig. 2). The structure of the stand is one of multi-stemmed clumps arising from the stumps of earlier mature trees. The capacity of mature birch to produce post-disturbance sprouts decreases after 40-60 years, and by age 100 only about one-half of the cut trees appear to produce basal sprouts (J. Zasada, unpubl).

In order to obtain stands with a structure and density similar to aspen, it is necessary for seed reproduction to fill in the gaps between the multi-stemmed groups. Birch produces vast quantities of seed at frequent intervals (Zasada and Gregory 1972). Establishment of seedlings is greatest on mineral soil but can occur on disturbed organic matter. Growth of seedlings is slower than sprouts. Unpublished data collected at Bonanza Creek Experimental Forest indicated that average seedling height in clearcuts was about 70 cm and maximum height about 1.2 m at age 5. Birch sprouts in the same area averaged 3-4 m.

Available moose browse varied from 4 kg/ha at the 1-year-old BC stand to 154 kg/ha at W-4. No birch browse was available in the 50-year-old birch stand. With the exception of stand W-4, browse production was mostly produced by sprouts. At W-4, the most productive in terms of available birch browse, the stand was composed entirely of stems resulting from seed regeneration. J. Oldemeyer (pers. communication) recorded an annual production of from 79 to 151 kg/ha of browse in 25-year-old birch stands on the Kenai National Moose Range.

Willow: Willows are primary forage species following disturbance in black spruce communities on uplands and on newly formed sandbars of flood plains. Although there is some overlap in species composition between uplands and lowlands, the sites in this study had only feltleaf willow occurring on both general types. Willow stand formation on uplands following

fire tends to be predominantly from sprouting. Sprouts can attain heights of 50 to 80 cm in 1 year, while seedlings take at least 3 years to attain this height. Stand formation on floodplains is a mixture of stems formed from seed and buried branches. In the case of sandbar willow, additional stems are produced by root suckering.

On upland sites, where Scouler willow predominated, stems were available above snowline the first 2 years after fire, but these were completely consumed by snowshoes hares (Wolff 1977). Four years after the fire, browse production was twice as great in the burn as in the unburned stand; 7 years after the fire, it was five times greater. Willow browse at MD-1 (birch) was less than at W-1 (willow) and probably reached peak production between 15 and 19 years post-fire. It is projected that browse production in W-1 will peak between 10 and 15 years after the fire and decrease by 20 years.

At TR 1, a flooplain site, browse production increased from 8 to 11 years, and it appeared to peak between 10 and 11 years. In the adjacent 28-year-old alder stand, TR-2, willow production was negligible, and alder was dominant. Alder was invading the 11-year-old stand, and it is projected that TR-1 will be dominated by alder and balsam poplar by 20-25 years.

A similar pattern of production and succession was evident at TR-3. Production declined between ages 16 and 19. Alder was beginning to invade this stand; according to the predicted successional pattern for the flood plain, it will dominate the stand along with poplar in the next 10 to 15 years (Viereck 1970).

In unpublished work we assessed sprouting capacity (rate of secondary succession) of floodplain willows by conducting a cutting study at TR-1. All willow stems were cut from four, 100-m^2 plots. Stem density and browse production were determined in May 1975 (before cutting), May 1976 (1 year after cutting), and May 1978 (3 years after cutting).

Cutting resulted in a 36% reduction in the number of willow stems per plot after 3 years. The number of shoots per shrub increased by 29 and 56% 1 and 3 years respectively after cutting. Browse production was 82% of predisturbance condition after 1 year and slightly greater 3 years after clipping (Table 4). These results indicated that the species on this floodplain site respond in a manner similar to that of willow on uplands.

Table 4. Response of Willows at Tanana River-1 Site to Removal of Above Ground Stems. N=4

Years since cutting	Stems per plot	Twigs per shrub	Browse per plot[1/]
Before cutting	253(42)[2/]	1.9(.3)	.37(.02)
1	154(24)	2.4(.4)	.30(.04)
3	161(27)	3.1(.5)	.40(.05)

1/ Multiply by 100 for kg/ha.

2/ Standard error of the mean of parentheses.

Browse Preference: Browsing preferences were difficult to obtain because of homogeneity of stands. Over the 4-year sampling period at TR-1, a preference was shown for sandbar willow followed by feltleaf willow and balsam poplar. At TR-3, feltleaf willow was preferred over tall blueberry willow, park willow, and balsam poplar (Table 3). Willows were preferred to birch in the mixed stand at MD-2 and W-4. In Quebec, Joyal (1976) also found willow to be preferred over aspen and birch. In the one instance where aspen occurred in mixture (W-4), it

was preferred to birch. Oldemeyer et al. (1977) found that alder and birch supply higher winter levels of protein, but willow is more digestible; because of variation in nutrients, trace elements, and digestibility among species, they suggest that variety is important in the diet of moose.

Preference for a species was dependent in part by its abundance in the stand. When willow had a low frequency of occurrence, it had a higher selective value than when it occurred in higher densities (Figure 3a). Preference indices using number of stems, branches, or biomass gave a similar result. The same pattern did not, however, hold for birch (Figure 3b). Small sample size prevented statistical analysis of these differences.

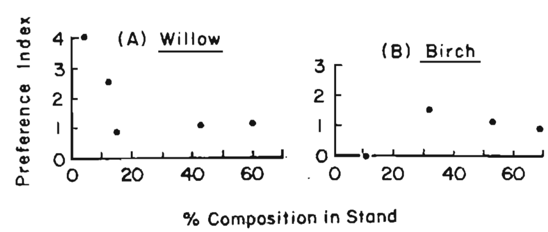

Figure 3. The relationship between percent composition in the stand of willows (A) and birch (B) and moose preference indices.

Due to low browsing intensities in most stands throughout this study, it was difficult to obtain a quantitative measure of browse preferences or even stand-type preferences. Browsing intensities were high at Bonanza Creek, but this was a small stand, and stands within 200 m experienced lower browsing intensities. In larger stands such as the Murphy Dome or Wickersham sites, moose had unlimited forage and could be more selective. In fact in W-2 (willow) browsing by moose was not recorded at 7 years, but browsing in W-1 (willow) was 19%. On the Kenai National Moose Range where moose populations are high and food is limited, all browse plant species are consumed at high levels (Oldemeyer et al. 1977). Similar observations were made in McKinley National Park from 1975 to 1978 where a high moose population has been browsing over 80% of preferred willow species (J. Wolff, unpubl).

Using data in this study and unpublished observations, we have attempted to list the browse species preferences. Sandbar willow is the preferred species followed by other willow species, birch, aspen, cottonwood, poplar, highbush cranberry, and alder. Willow species, which are common in interior Alaska and are used extensively by moose, include *S. alaxensis*, *S. planifolia*, and *S. arbusculoides* (Milke 1969, Machida 1979). Alder was reported consumed by moose along the Colville River on the North Slope of Alaska (Coady 1974).

In this study, no attempt has been made to determine palatability of individual shrubs other than developing a preference index for each species. Nonrandom browsing by moose on individuals within a species has been suggested by LeReseche and Davis (1971) and was quantified by Machida (1979). The nutrient content, digestibility, and inhibitory compounds which are present in different concentrations in different species and between shrubs within a species have an effect on palatability (Cowan et al. 1950, Oldemeyer et al. 1977). Shrubs which have been browsed for several consecutive years may contain inhibitory compounds which reduce palatability and inhibit further browsing; however, Machida

(1979) found that moose may select the same shrub for at least 3 consecutive years to the exclusion of others. Therefore, only a portion of the biomass of browse available in a stand may be palatable to moose.

Carrying capacity and utilization of browse in a stand was computed using an average daily consumption rate of 5 kg browse/moose/day (Gasaway and Coady 1974) and recorded in moose days per hectare (M.D./ha) (Wolff 1978). Carrying capacities and utilization for all stands which produced woody browse are shown in Figure 4 and Table 5. Maximum carrying capacity is based on a daily consumption rate of 5 kg/moose assuming *all* browse available is palatable. In this study, a maximum browsing intensity of 56% was recorded. On the Kenai National Moose Range, J. Oldemeyer (pers. communication) found that moose which were taking 85% of the available browse were starving and were undergoing high over-winter mortality. In McKinley National Park, I recorded a browsing intensity of between 80% and 90%; calf production and winter calf survival there were low (S. Buskirk, National Park Service, McKinley National Park, Alaska, pers. comm.). Therefore, at a browsing intensity of between 60% and 85%, moose are probably reaching the carrying capacity of palatable browse. Based on these figures and observations, we have adjusted the carrying capacity of palatable browse to 75% of total browse available which probably represents the critical threshold in most stands below which moose can still select palatable browse. After 75% of the browse has been consumed, the remaining browse is not only less nutritious but more scattered and energetically more costly for the moose to locate and consume the remaining 25%. The maximum sustained browsing intensity which a shrub can withstand is probably between 50% and 75% (Krefting et al. 1966, Wolff 1978). The 75% adjusted carrying capacity must be

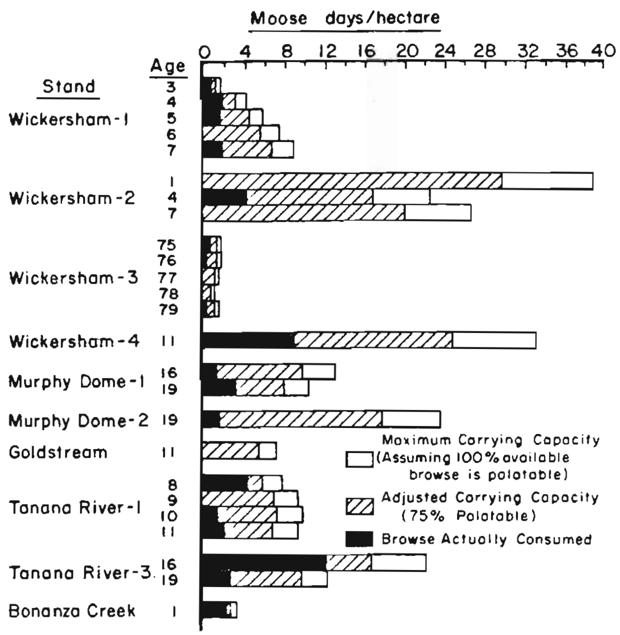

Figure 4. Maximum and adjusted carrying capacities and amounts of browse consumed by moose in each study area.

considered a generalization and should be further adjusted to specific stand conditions.

Moose population densities during the period of this study (1972-1978) were not measured for the study sites. However, during this period populations were generally considered very low (Coady 1976). The implications of these low populations to browse utilization are two-fold. The most obvious is the relatively low level of browse utilized. During the course of this study, all areas observed had been browsed to some degree during at least 1 year. With several exceptions, however,

Table 5. Carrying Capacity and Browse Utilization for Selected Upland and Flood Plain Stands in the Tanana River Drainage.

Stand	Age	Browse available Kg/ha	Maximum carrying capacity M.D./ha	Adjusted carrying capacity M.D./ha	Total browse consumed Kg/ha	Actual utilization M.D./ha
Wickersham-1	+3	6.5	1.3	1.0	2.9	0.6
	+4	19.3	3.9	2.9	8.7	1.7
	+5	28.5	5.7	4.3	7.4	1.5
	+6	37.1	7.4	5.6	0	0
	+7	44.1	8.8	6.6	8.4	1.7
Wickersham-2	+1	198.4	39.7	29.8	0	0
	+4	112.9	22.6	17.0	21.5	4.3
	+7	134.2	26.8	20.1	0	0
Wickersham-3	+7	9.5	1.9	1.4	3.2	0.6
	+76	9.5	1.9	1.4	0.8	0.2
	+77	8.5	1.7	1.3	0	0
	+78	6.6	1.3	1.0	0	0
	+79	8.3	1.7	1.3	0.8	0.2
Wickersham-4	+11	167.0	33.4	25.1	44.8	9.0
Murphy Dome-1	+16	65.9	13.2	9.9	5.5	1.1
	+19	52.4	10.5	7.9	15.5	3.1
Murphy Dome-2	+19	119.7	23.9	17.9	7.3	1.5
Goldstream	+11	35.9	7.2	5.4	0	0
Tanana River-1	+8	39.8	8.0	6.0	22.4	4.5
	+9	47.6	9.5	7.1	0	0
	+10	50.0	10.0	7.5	8.0	1.6
	+11	48.0	9.6	7.2	10.5	2.1
Tanana River-3	+16	112.5	22.5	16.9	61.7	12.3
	+19	62.7	12.5	9.9	12.9	2.6
Bonanza Creek	+1	1 16.1	3.2	2.4	13.0	2.6

browsing intensities were generally less than 50 percent; and in four stands no browsing was observed. Although carrying capacity is not known for large areas within this region, the data suggest that moose have not been food-limited, and much winter range is not being exploited.

Secondly, moderate browsing intensities on trees and woody shrubs in young stands may actually increase the amount of browse in future years (Spencer and Chatelain 1953, Krefting et al. 1966). Wolff (1978) observed that browsing has a pruning effect in that browsed branches produced more vegetative growth the following growing season than unbrowsed branches. This is true for young and old stands but has a greater positive effect on young shrubs or trees. Multiple stems and lateral branching of main stems of willows at Wickersham are the result of heavy browsing by hares and moose the first 3 years after fire. The large number of twigs per stem of birch at W-4 and Murphy Dome are likewise the result of a brooming effect following several consecutive years of browsing on terminal shoots. Browsing had not occurred at the Goldstream site for several years, and current annual growth on willows was less than 0.7 g/twig. Current annual growth in browsed stands was greater than 1.0 g/twig; Wolff (1978) reported current annual growth of browsed twigs at W-1 to be 4.0 g/twig. Heavy browsing intensity near 100% for several years may, however, lower current annual growth and in some cases kill the plant.

SUMMARY AND CONCLUSIONS

1. Seral communities important to moose winter range production result from both primary and secondary succession. The most common cause of the latter is wildfire; however, forest harvesting and land clearing also fall into this category. Primary succession occurs on newly deposited sandbars along the Tanana River and its tributaries.

2. The dominant trees and shrubs in these seral communities are several species of willow, birch, aspen, balsam poplar and alder. All of these species, but particularly aspen, are capable of producing some browse within one growing season after disturbance, provided that vegetative regeneration is possible. If they must regenerate from seed, a minimum of 3-5 years is required before browse production begins.

3. The time of maximum production varies with species, site conditions, and severity of disturbance. Aspen sucker stands are most productive up to 10 years old. Willow sprout stands reach maximum production between 10 and 16 years with a marked decline after 20 years. Birch is similar to willow.

4. During peak production, aspen stands appear to produce more biomass followed by birch and willow, in that order. This is probably due to the dense aspen stands formed by root suckers.

5. One or more willow species are preferred to birch, aspen, balsam poplar, and alder.

6. The realized carrying capacity of a stand may be only 75 percent of total browse available.

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