

FOREST DISTURBANCE TYPE DIFFERENTIALLY AFFECTS SEASONAL MOOSE FORAGE

R. A. Lautenschlager¹, Hewlette S. Crawford², Martin R. Stokes³ and Timothy L. Stone⁴

¹Ontario Ministry of Natural Resources, Ontario Forest Research Institute, 1235 Queen St. East, Sault Ste. Marie, Ont., P6A 5N5; ²Crawford Associates, R.R. 01, Box 1170, East Eddington, Maine 04428; ³Dept. of Animal, Veterinary and Aquatic Sciences, University of Maine, Orono, Maine 04469; ⁴USDA Forest Service, Northeastern Forest Experiment Station, RR 1, Box 589, Bradley, Maine 04411.

ABSTRACT: We examined the effects of forest disturbance on forage availability, moose (*Alces alces*) seasonal forage selection, and predicted *in vivo* digestibility in eastern Maine. Wet-mass estimates and dry-mass conversions of species consumed by 3 tamed moose were made throughout the year (late winter, early spring, late spring, summer, fall, early winter) in budworm (*Choristoneura fumiferana*) defoliated, defoliated-clearcut, defoliated-clearcut-burned, and undefoliated (control) 60- to 80-year-old spruce-fir (*Picea-Abies*) stands. Four treatment replicates were on sandy (deep) and 2 on silty (shallow) soils. Three plots also were established on sandy soils within both 5- and 14-year-old wildfire burns. Diet samples mixed in the proportions eaten in the field and representing the species and plant parts eaten during 564 individual feeding bouts were digested (*in vitro*) with cattle rumen fluid, and converted to *in vivo* digestibility estimates using forages of known *in vivo* digestibility. Forage dry mass consumption and forage group selection was related to treatment, season, and with few exceptions, availability. Dry mass consumed ranged from 152 g/hr (early winter on controls) to 1,320 g/hr (summer on the 14-year-old wildfire). Digestibility of mixed diet samples changed during the growing season, but not during the dormant (November to April) period. Digestibility ranged from 29% [early spring (pre-leaf-out) on the 14-year-old wildfire] to 47% [fall (80) on defoliated-clearcut and defoliated-clearcut-burned (combined) and late spring (post-leaf-out) on the 5-year-old wildfire]. Deciduous woody species were the forage group most commonly eaten, accounting for: 15 to 70% (depending on season) of the forage consumed in controls; 25 to 70% in budworm defoliated stands; 50 to 85% in the "recently disturbed" (clearcut, clearcut and burned, 5-year-old wildfire); and 80% or greater throughout the year in the 14-year-old wildfire plots. Moose ate significant amounts of previously unobserved or what have been considered insignificant forage groups [fallen hardwood leaves, ferns, *Rubus* spp., and spruce (*Picea* spp.)].

Natural and human-caused disturbances differ in their effects on forage production and moose use. Control and budworm defoliated plots, through time, produced limited amounts of the least digestible forage. Forage production and digestibility following cutting and controlled burns were similar, and greater than that on control and budworm defoliated plots. Although the 14-year-old wildfire produced the greatest amount of available forage, digestibility was similar to that observed on control and budworm defoliated plots. Forage production, up to 6 growing-seasons post-treatment, was reduced more by wildfires than the other disturbances examined.

ALCES VOL. 33 (1997) pp.49-73

Disturbances, like forest harvesting, fire, and spruce budworm (*Choristoneura fumiferana*) damage can reduce mature forest stands to pioneer successional communities favorable for moose (*Alces alces*) (Peterson 1955, Bendell 1974, Peek 1974). Krefting's (1974) suggestion that timber cut-

ting is the most important factor improving moose habitat is commonly cited as the reason for increasing moose populations where cutting has been extensive. Bendell (1974) suggested that the effects of burning and logging are similar. Haggstrom and Kelleyhouse (1996), who discussed effects

of forest management, including cutting, wildfires, and controlled burns, on a variety of wildlife, recommend controlled burns following clearcutting to enhance the growth of early successional plants preferred by early successional wildlife species. There is, however, little empirical data comparing the effects of natural and human-caused disturbances on wildlife in general, or moose in particular.

Like fire and timber harvesting, spruce budworm defoliation can substantially affect forest composition, initiate secondary succession, and produce habitat changes. In addition, Hansen *et al.* (1973) noted that budworm damaged forests provide ideal fuel for fires, which can return large areas to early successional high browse-producing shrub stages. Vegetation production in any area, however, is also related to site quality (Spurr and Barnes 1980); site quality, in turn, can affect forage quality, for instance Crawford *et al.* (1993) reported that white-tailed deer (*Odocoileus virginianus*) found more desirable foods on deep ("sandy") than shallow ("silty") soils in Maine.

A major spruce budworm infestation began in Maine in 1974. At that time landowners increased the harvest of spruce (*Picea* spp.) and balsam fir (*Abies balsamea*) (Edson 1983) in order to save damaged timber and remove threatened stands (Dines and Tomblor 1983). This infestation presented an ideal opportunity to study the simultaneous effects of several types of forest disturbance, both natural and human-caused, on vegetation production, moose forage use, and the digestibility of forages selected. Our objectives were to compare and contrast vegetation production, seasonal forage selection, mass consumption, and digestibility of mixed diets selected by moose while feeding on sandy and silty soils following spruce budworm damage, related cutting and burning, and wildfires in eastern Maine. An earlier overview paper (Crawford *et al.* 1993)

summarized effects of defoliation, cutting, cutting followed by controlled burning, and no budworm damage (control) on digestible energy obtained by moose and white-tailed deer during this study. Here we present more detailed information about forage: (1) availability, (2) groups and species eaten, (3) mass consumption, and (4) digestibility as it relates to these natural and human caused disturbances.

METHODS

Study Area

This study was conducted in Washington and Hancock Counties in eastern Maine. Seven of the 10 blocks examined during this study were established on the Moosehorn National Wildlife Refuge (MNWR -- 45° 08'N, 67° 19'W), located in Washington County, approximately 7 km south of Calais, Maine (Fig. 1). The main experiment (6 blocks), which included the manipulative treatments (cutting, controlled burning), took place on the MNWR. Because all spruce-fir forests on the MNWR were defoliated at the time the experiment was established, control (CONT) blocks (2) were established in the closest accessible mature (60-80-year-old), undefoliated spruce-fir (> 50% basal area balsam fir) forests available (southern Hancock County, approximately 130 km southwest of the MNWR).

As an adjunct to the main experiment, to help quantify the longer term response of local plant communities and moose to wildfire and aid comparisons between human-caused and natural disturbances, we established blocks in nearby areas burnt by wildfires. These blocks were located centrally in a representative portion of a 5-yr-old wildfire (5-BURN) (1 block) and a 14-yr-old wildfire (14-BURN) (1 block); the 5-BURN was approximately 35 km south of the MNWR and the 14-BURN was on the MNWR (Fig. 1).

The MNWR is within the Southern Inte-

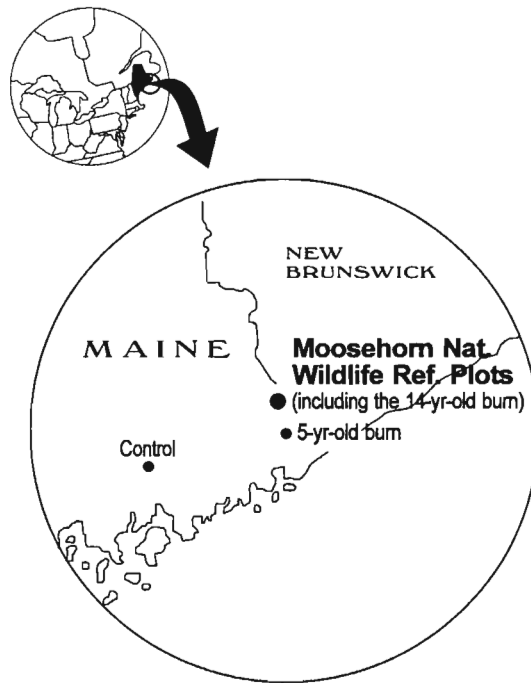


Fig. 1. Study area locations in eastern Maine.

rior Climatic Division and the 5-BURN and CONT are within the Coastal Climatic Division. Both divisions are characterized by changeable weather, large temperature ranges (diurnal and annual), precipitation which is rather evenly distributed throughout the year, and cool summers with a May-September growing season (Lautzenheiser 1972). The entire area is within the sub-boreal forest which has been called the: "Boreal Mixedwood" (MacDonald 1995), "Closed Boreal/Northern Hardwood-Conifer" (Aldrich 1963), and "Acadian" (Rowe 1972) forest.

The main experiment consisted of 6 4-8 ha study blocks established in the MNWR, where spruce budworm damage had caused extensive mortality in spruce-fir stands. Blocks were placed on both "silty" (shallow - 2 blocks) and "sandy" (deep - 4 blocks) soils (Tables 1 and 2). All soils were glacially derived and included some rock outcrops. The silty, commonly poorly-drained, shallow soils were mostly a Lyman-Tunbridge complex or a Tunbridge-Peru complex, and depths of solum were generally less than 1 m. The sandy, well-drained, deep soils were Buxton and occasional pockets of Scantic, and Croghan-Adams complex with Adams soils on higher elevations. These soils were 1.5 m or more deep (Crawford *et al.* 1993). Blocks were established between 1977 and 1979 in balsam fir and spruce stands containing > 50% basal area balsam fir showing moderate upper-crown and light mid-crown spruce budworm defoliation. Budworm defoliation began in this area in 1974 and continued through 1981, by which time most of the balsam fir and much of the spruce were killed.

Treatments

Each block was a contiguous unit and consisted of 3 1-2 ha plots. Each block in the main experiment contained: defoliated (DEF); defoliated and clearcut (CUT); and defoliated, clearcut and burned (CUT-BURN) treatment plots. Cutting was completed in summer 1979, and all burning took place in the spring of 1980. Control (CONT) blocks,

Table 1. Number of replicates, by soil type and treatment, for moose feeding following forest disturbances in eastern Maine.

Soil	Defoliated	Def./Cut	Def./Cut/ Burned	5-Yr-old Wildfire ¹	14-Yr-old Wildfire ¹	Control ¹
Sandy	4	4	4	3	3	3
Silty	2	2	2	- ²	-	3

¹Not true replicates, rather these areas were single blocks divided into thirds for sampling.

²No plots located on this soil type.

Table 2. Number of moose feeding bouts observed and mixed diets analyzed by treatment, soil type and feeding period in eastern Maine.

Feeding Period	Soil Type	Defoliated	Def. & Cut	Def., Cut & Burned	5-Yr-old Wildfire	14-Yr-old Wildfire	Control
Fall (1980)	Silty	6 ³	6	6	- ⁴	-	9
	Sandy	12	12	12	9	9	9
Early Winter	Silty	6	6	6	-	-	No Obs.
	Sandy	12	12	12	6	9	6
Late Winter (1981)	Silty	6	6	6	-	-	6
	Sandy	12	12	12	No Obs	9	6
Early Spring	Silty	6	6	6	-	-	6
	Sandy	12	12	12	6	9	6
Late Spring	Silty	6	6	6	-	-	6
	Sandy	12	12	12	6	9	6
Summer	Silty	6	6	6	-	-	6
	Sandy	12	12	12	9	6	
Fall (1981)	Silty	6	6	6	-	-	6
	Sandy	12	12	12	6	9	6
Total		126	126	126	39	63	84

¹Three moose on 2 defoliated silty plots during the fall feeding period.

²No plots located on this soil type.

one on sandy and the other on silty soil, each containing 3 adjacent replicate plots, were established in the closest accessible mature undefoliated spruce-fir forests available (Fig. 1). Blocks, containing 3 adjacent replicate plots, were also located centrally in a representative portion of a 5-yr-old wildfire (5-BURN, 1 block) and a 14-yr-old wildfire (14-BURN, 1 block). Both wildfire blocks were on sandy soils (Table 1). Crawford *et al.* (1993) provide additional details about soils, vegetation composition, and the controlled burns examined in this study.

Vegetation Sampling

Standing mass of herbaceous vegetation and woody shoots < 1.3 cm in diameter (considered available forage) was sampled on all plots between July and September during 1980 and 1981. Mass (kg/ha) of vegetation was determined on 10 randomly located temporary and 10 randomly established permanent quadrats (5.0 x 0.5 x 2.5 m) on each plot. Mass measurements were stratified vertically into 0 to 0.5 m, > 0.5 to 1.5 m, and > 1.5 to 2.5 m above ground. Two methods of sampling were used: stratified weight estimate for which separate ratio es-

timators were calculated for estimated weights < 50 g and > 50 g, otherwise the technique was similar to Crawford (1971); and microwave signal attenuation (Crawford and Stutzman 1983). From 0 to 0.5 m above ground the stratified mass-estimated system was used. If either of the two vertical strata above the lowest stratum contained more than 50 g of vegetation, a microwave link was set up on each end of the 5-m-long quadrat and signal loss caused by the vegetation was determined. When microwave attenuation was used, we visually estimated the percent composition by plant species in the signal path since signal loss determines only total vegetation mass.

Following these estimates, 2, chosen at random, of the 10 temporary quadrats in each plot were clipped in order to record fresh and oven-dry weight of vegetation by species. Vegetation samples from these quadrats were collected and oven dried at 65°C to a constant weight. Estimated weights and reduced microwave signal strength were regressed on fresh and oven-dry weights to derive formu-

lae to convert estimates to actual weights. Permanent quadrats were not clipped.

Feeding Observations and Vegetation Collections

Three moose, 2 females, 2 and 4 years old, and a 3-year-old neutered male, were reared, maintained, and trained using the techniques of Lautenschlager and Crawford (1983). They were transported to and from blocks in a horse trailer. When not feeding on study blocks they were held in pens, which contained woody and herbaceous browse, and fed a pelleted dairy ration ad libitum. Feeding observations (bouts) and vegetation collection replicates (Table 1) were conducted during 6 feeding periods (Table 2, Fig. 2): fall (1 September to 31 October, 1980 and 1981), early winter (1 November to 31 December, 1981); late winter (1 January to 19 March, 1981), early spring (20 March to 30 April, 1981), late spring (1 May to 30 June, 1981), and summer (1 July to 31 August, 1981). Feeding periods were based on expected plant phenological differences, and

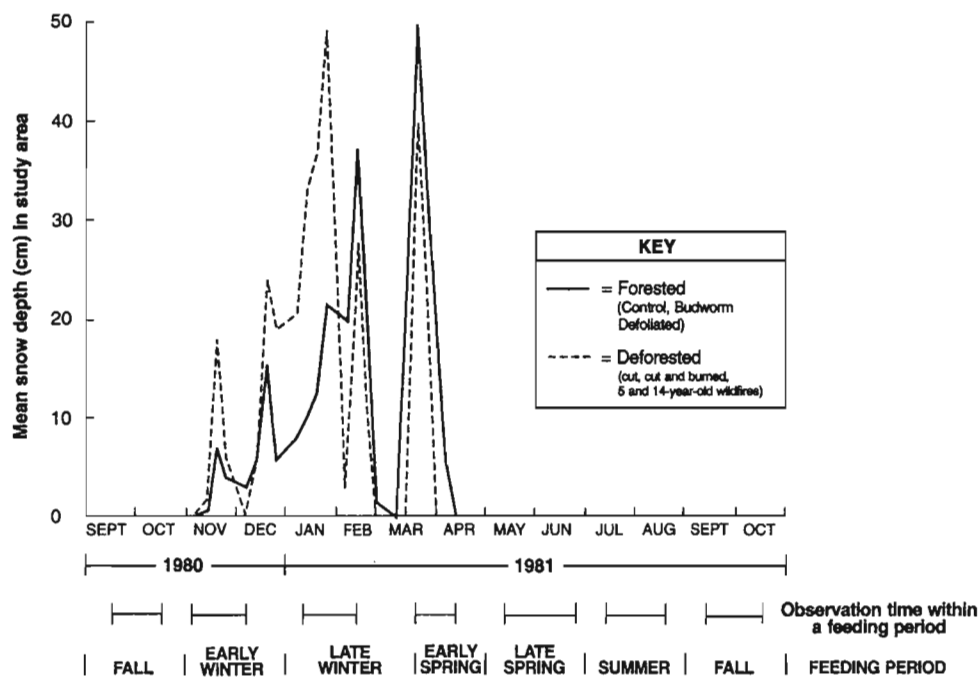


Fig. 2. Feeding and sampling periods, and snowcover by treatment related cover type.

winter feeding periods had unique snow depth characteristics (Fig. 2). No data were recorded during the summer of 1980 (Table 2); during that time observers refined their techniques, and moose feed on all plots, became accustomed to the area, available foods, transport, and confinement routines.

Observers were trained to estimate the wet mass of plants selected by the moose and were checked for accuracy during each feeding period. Accuracy checks consisted of repeated simulated foraging by one crew member while an observer estimated wet mass of each simulated bite. The observer's wet mass estimates were later regressed against actual wet mass, recorded at that time, to provide correction coefficients.

The sampling crew of 3 handled the moose and observed foods selected. Handlers accompanied each animal to each plot for 0.5 hr during each feeding bout. Plots within a block were visited at random during early morning, late afternoon, and evening. Once on a plot animals were allowed to feed and move freely and were redirected only when they attempted to leave the plot. Observers estimated the wet mass of alternate bites, by species of plants eaten, and collected 5- to 50-g (wet mass) samples of each plant eaten during every feeding bout. When possible, similar reproductive and vegetative parts were collected from the same plant selected by the moose; otherwise similar plant parts were taken from the same species, close to where the feeding took place. Foraging information was dictated into a portable tape recorder, or more commonly to an assistant who recorded it on computer readable data sheets (Lautenschlager 1984). After the first moose fed and vegetation was collected, the procedure was repeated with the remaining 2 moose. Feeding bouts were timed, and if an animal stopped feeding before the end of a bout it was allowed to rest; the observation continued when that animal began feeding again. Animals were moved to a new plot

and the procedure was repeated only after each had time for rumination and rest. This produced a feeding intensity of 9 moose hours/plot/year, i.e., 3 (moose) x 0.5 (hours/bout) x 6 (bouts/year). Mean forage consumption (Table 3) was based on wet mass estimates converted to dry mass values using a conversion factor developed from drying forage picked during feeding bouts.

Forage Quality

A representative sample of plant species and parts eaten on each plot was oven dried at 60°C to a constant mass, ground in a Wiley mill through a 1-mm mesh screen and stored in airtight plastic bags. Dried samples of plants that made up the top 90 to 100 percent by mass were combined to represent mixed wet-mass diets selected during each feeding bout. Digestible dry matter (DDM) of mixed diets was determined with bovine rumen fluid (Crawford and Hankinson 1984) by a 2-stage in vitro technique (Tilley and Terry 1963) modified by Palmer *et al.* (1976). Standard reference forages of known digestibility for white-tailed deer, provided by R. L. Cowan of the Pennsylvania State University, were used to convert in vitro DDM values to in vivo (Palmer and Cowan 1980) estimates. Because no source of standard reference forages for moose was available, we used bovine rumen fluid and deer standards, assuming that digestibility of forages selected by moose would be closer to digestibility values of deer than those of cattle. Caloric values were determined by bomb calorimetry (AOAC 1975).

Nomenclature and Analysis

Common and scientific names follow Fernald (1970). All statistical tests are based on t-tests, considered significant at $P < 0.05$, and confidence interval ($x \pm 2SE$) comparisons, as recommended by Schaubert and Edge (1995).

Table 3. Gram dry mass [\bar{x} + SE (N)] of forage consumed/0.5 hr feeding bout¹, by treatment and season in eastern Maine.

Feeding Period	Treatments				Total
	Control ²	Defoliated	REC-DIST	14-BURN	
Fall (1980)	87.4+19.6 (18)	152.3+28.4 (18)	142.4+12.1 (45)	212.9+49.2 (9)	148.8
Early Winter	37.7+6.5 (6)	46.4+7.4 (18)	75.8+5.9 (42)	57.1+7.0 (9)	54.3
Late Winter (1981)	172.4+20.2 (12)	159.2+22.6 (18)	134.9+13.0 (36)	219.5+25.1 (9)	171.5
Early Spring	55.9+7.9 (12)	111.8+11.1 (18)	88.0+6.5 (42)	87.0+10.1 (9)	85.7
Late Spring	69.2+13.3 (12)	124.5+17.9 (18)	111.8+7.6 (42)	200.5+25.9 (9)	126.5
Summer	146.5+20.7 (12)	237.6+19.0 (18)	239.9+15.6 (42)	329.6+25.9 (9)	238.4
Fall (1981)	78.4+14.7 (12)	171.6+23.1 (18)	201.5+14.0 (42)	253.1+24.4 (9)	176.2
Total (\bar{x})	92.5	143.3	142.0	194.3	

¹Every other bit recorded, therefore **hourly consumption = 4 X the consumption rate given.**

²Control = 60- to 80-year-old spruce-fir forests; Defoliated = spruce budworm defoliated spruce-fir stands; REC-DIST = includes defoliated and clearcut (CUT), and defoliated, clearcut, and burned (CUT-BURN); and the 5-BURN (an area burned by a wildfire 5 years before the study began); 14-BURN = an area burned by a wildfire 14 years before the study began.

RESULTS

More than 100 species and generic groups, such as *Salix* spp., were eaten during this study. Availability and use of individual species and generic groups varied by treatment and feeding period (6 "seasons") within the year. To provide a general understanding of seasonal use patterns, individual species and generic groups were combined into forage groups of similar species or groups (Appendix I). In addition, soil treatments were combined for comparison.

Even though we found significantly more forage available on sandy than silty soils (Crawford *et al.* 1993), moose dry matter consumption and DDM seldom showed sta-

tistically significant differences between soil types (1 of 27 and 2 of 27 comparisons, respectively - Lautenschlager, unpublished).

In addition, because out of 14 comparisons (in which soil types were examined separately) no statistically significant differences in dry matter consumption nor DDM were identified between CUT and CUT-BURN treatments and because forage group selection following these treatments was similar (Appendix I), CUT and CUT-BURN treatments were combined into a recently disturbed (REC-DIST(-)) treatment group (Table 4). The 5-BURN was included in the REC-DIST treatment group when parameter treatment means were similar to those of

CUT and CUT-BURN [forage consumption (Table 3), forage availability (Table 5)], but presented separately [DDM (Table 6)] when means were different.

Forage consumption (Table 3) varied significantly among treatment types and seasons. Mean dry mass consumed ranged from 38g/feeding bout (152g/hr) on the CONT treatment in early winter to 330g/feeding bout (1,320g/hr) on the 14-BURN during the summer. Predicted in vivo DDM also varied significantly by season on all treatments (Table 6, Fig.'s 3 to 6). Forage was least digestible (=34.4%) during the dormant period (early winter, late winter, early spring), had highest DDM during late spring (=43.7%), and intermediate DDM values during summer and fall (=39.4%) (Table 6). Forage availability (0 to 2.5 m) was lowest on CONT and highest on the 14-BURN plots (Table 5). Availability on REC-DIST (CUT, CUT-BURN, 5-BURN) treatments was similar and was >2 times that on the DEF. Availability on the DEF plots decreased significantly from 1980 to 1981 (Table 5) due primarily to spruce budworm-caused mortality of the near-ground balsam fir (*Abies balsamea*) and spruce (*Picea* spp.) advance regeneration. Moose feeding, on the limited amount of near-ground conifer biomass in these plots,

may also have contributed to that reduction.

Analysis by Feeding Period

Fall

Where available, moose concentrated on deciduous species that retained leaves in the fall (1980 and 1981). Although there was considerable variation among treatments in species selected, species most commonly eaten within the deciduous forage group during this period included: quaking aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), pin cherry (*Prunus pensylvanica*), beaked hazel (*Corylus cornuta*), red maple (*Acer rubra*), and willow (*Salix* spp.). Fibrous forbs (Appendix I') were important fall foods wherever forest canopies were relatively intact or intact (DEF and CONT - Fig.'s 3 and 6), and minimal amounts of deciduous species were available (Table 5). There was little difference in fibrous forb use on CONT plots between the 2 fall periods examined (1980, 1981), but on DEF plots, although availability remained essentially unchanged (Table 5), use decreased from 8% during 1980 to about 0.5% during 1981. This decrease in fibrous forb use was offset by an increase in *Rubus* use, related to its increased availability associated with continuing defoliation (Table 5), and

Table 4. Treatment abbreviations and combinations discussed in this paper.

CONT = 60-80-year-old undefoliated spruce-fir forest
DEF = Spruce budworm defoliated (Defoliated)
CUT = Defoliated and clearcut
CUT-BURN = Defoliated, clearcut, and burned
5-BURN = 5-year-old wildfire
14-BURN = 14-year-old wildfire
Combinations:
REC-DIST = CUT, CUT-BURN, and 5-BURN
REC-DIST (-) = CUT and CUT-BURN
Forested = CONT and DEF
Deforested = CUT, CUT-BURN, 5-BURN, and 14-BURN

Table 5. Mean forage availability [average grams (wet mass)/m² from 0 to 2.5m above ground] in eastern Maine; measured during the growing season, and estimated, based on growing season measurements, for the dormant season.

	GROWING SEASON (Measurements)						14-BURN
	Control		Defoliated		REC-DIST ¹		
Forage Group	80	81	80	81	80	81	81
Fungi	10.5	3.2	1.2	0.8	0.1	0.2	- ¹
Lichens	1.1	2.0	7.6	11.3	7.6	7.6	trace ²
Ferns	1.6	0.3	12.3	6.8	42.2	29.8	5.5
Grass & Sedge	0.2	0.2	15.3	6.3	49.5	45.6	44.0
Conifer ³	21.8	22.5	113.6	50.4	8.7	15.0	65.0
Spruce	2.7	0.9	27.0	2.9	0.4	1.1	39.7
<i>Rubus</i> ⁴	trace	trace	11.2	33.3	5.3	71.5	27.1
Decidu.	2.0	3.6	22.0	21.9	144.4	148.3	366.5
Suc.for.	1.2	1.1	3.6	3.9	4.0	4.0	4.3
Fib.For.	1.8	1.3	11.4	13.7	102.8	74.0	43.2
Heath & Grn	0.1	0.4	1.2	1.3	2.0	2.1	2.6
Total	43.0	35.5	226.4	152.6	412.0	399.2	597.9

	Dormant Season (Estimates ⁶)						
Fungi	3.4	0.7	0.5	0.5	0.1	-	-
Lichens	0.5	1.0	3.1	3.2	3.0	2.7	trace
Conifer	17.6	19.8	83.0	24.7	1.4	2.1	40.1
Spruce	2.7	0.5	15.3	1.2	0.1	0.1	25.8
<i>Rubus</i> ⁷	-	-	0.5	4.1	2.9	5.6	1.0
Decidu.	0.4	0.6	3.2	4.1	17.9	29.5	75.2
Fib.For	-	-	0.1	0.2	5.5	5.4	4.9
Total	22.4	24.8	105.7	38.0	30.9	45.4	147.0

¹Not detected.

²Trace=less than 0.5 g/m².

³Conifer is predominately balsam fir (*Abies balsamea*), with a trace of eastern hemlock (*Tsuga canadensis*).

⁴Predominately red raspberry (*Rubus idaeus*).

⁵Includes members of the Heath Family, and low growing evergreen species.

⁶Forage available between 0.5 and 2.5 m.

⁷Weight mass estimate for *Rubus*, Deciduous and Fibrous Forbs based on 1/3 of growing season wet mass.

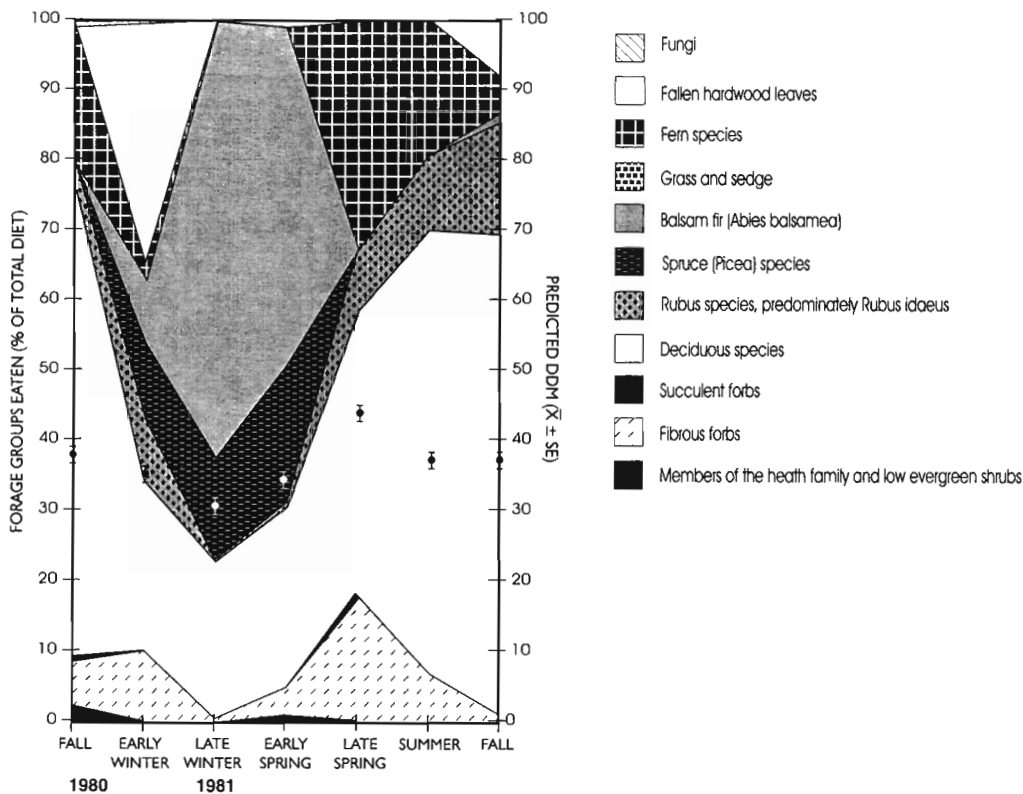


Fig. 3. Seasonal forage groups eaten (% of total diet), and predicted digestible dry matter (DDM ± SE) on the spruce budworm defoliated (DEF) treatment in eastern Maine.

an increased use of fallen hardwood leaves (mostly red maple, but some birch) in 1981. It is unclear why fallen hardwood leaves were eaten to a greater extent in 1981 than in 1980 (Fig. 3), but ferns, mostly bracken fern (*Pteridium aquilinum*) were eaten instead of fallen hardwood leaves in 1980.

Mean forage biomass consumption (Table 3) decreased on every treatment type between summer and fall 1981. It also decreased between the summer acclimation period in 1980, and that fall (Lautenschlager, unpublished). Mean forage biomass consumption on all disturbed sites [DEF, CUT, CUT-BURN, 5-BURN, 14-BURN) increased in 1981 over 1980 fall values (Table 3). Growing season forage availability on the CONT treatment decreased slightly from 1980 to 1981 (Table 5), and that decrease seems to be reflected in the slight reduction

in mean consumption in 1981.

Forage digestibility (DDM) was highly variable among treatments in the fall of 1980 and less so in 1981 (Table 6, Fig.'s 3-6). In 1980 the CONT treatment had the lowest DDM of any treatment, while REC-DIST(-) and the 5-BURN had significantly higher DDM than the other treatment. Forage digestibility on the REC-DIST(-), however, was significantly higher than any other treatment during the 1980 fall feeding period. Means of the other treatment types, DEF, and 14-BURN, were statistically similar during this period. Statistical differences among treatments seen in the fall of 1980 were no longer evident by the fall of 1981; by then mean DDM of forage on CONT increased significantly from 1980 means, while it decreased significantly from the 1980 mean on the REC-DIST(-) treatments. The dramatic

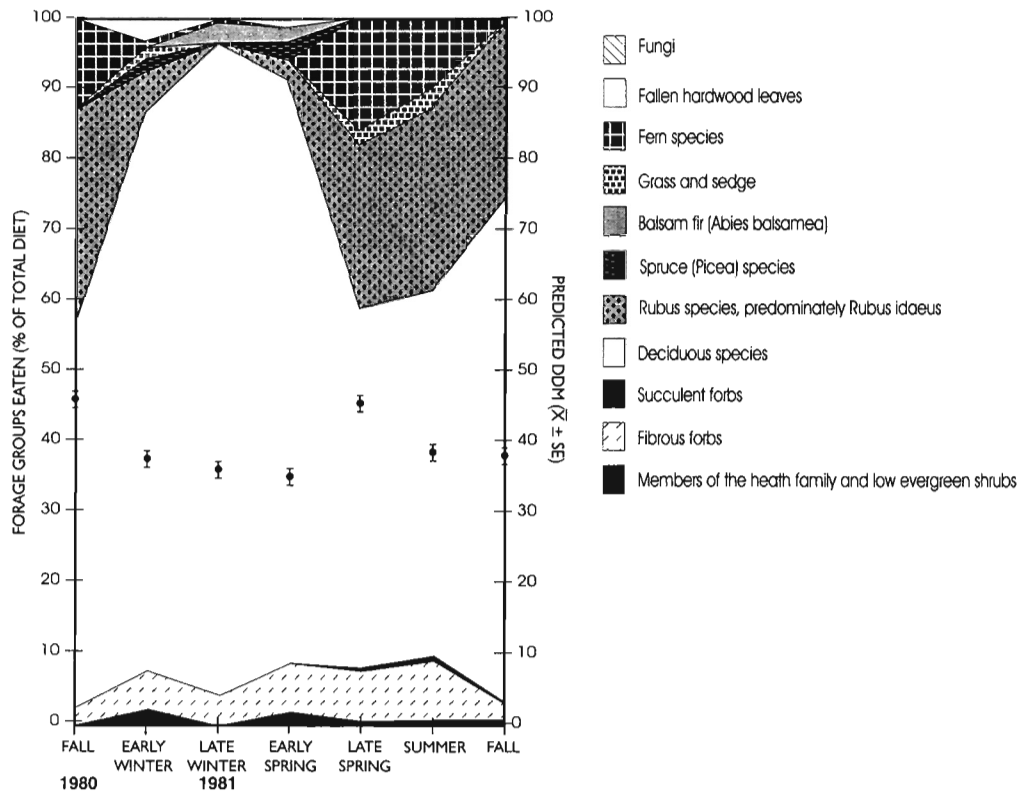


Fig. 4. Seasonal forage groups eaten (% of total diet), and predicted digestible dry matter (DDM \pm SE) on the recently disturbed [REC-DIST (defoliated and clearcut, defoliated, clearcut, and burned, and 5-year-old wildfire) treatments in eastern Maine.

increase in digestibility between 1980 and 1981 on CONT, seems associated with decreased use of deciduous species and increased use of fallen hardwood leaves (Fig 6); while the decreased digestibility on REC-DIST(-) during these periods seems associated with decreased use of fern species (Fig. 4).

Early Winter

Fir, and to a significantly lesser degree, spruce, became an important part of the diet in early winter; however, moose again concentrated on deciduous species when they were available (Fig.'s 3-6); everywhere except on the DEF and CONT plots (Table 5). Fallen hardwood leaves were also eaten in large amounts at this time, contributing 34% of the early winter diet on the DEF plots (Fig.

3) and 10% on the 14-BURN plots (Fig. 5), where an abundance of other forage groups were available (Table 5). Fibrous forbs, predominantly bunchberry (*Cornus canadensis*), were also important on the DEF, and to a lesser extent on the REC-DIST (Fig. 4), and 14-BURN (Fig. 5).

Forage consumption (Table 3) decreased significantly on all treatments during the early winter, to the lowest levels observed during this study. Early winter snow (Fig. 2) reduced the availability of some desirable food (Table 5), and caused animals to spend more time searching for less food.

Mean forage digestibility (DDM) decreased on all treatments between fall and early winter samples in 1980 (Table 6, Fig.'s 3-6); with statistically significant decreases on the REC-DIST(-), 5-BURN, and 14-

Table 6. Predicted in vivo digestible dry matter (DDM) [\bar{x} + SE (N)] in mixed diets selected, by treatment and season in eastern Maine.

Feeding Period	Treatments					Total
	Control ¹ *	Defoliated*	REC-DIST(-) ² *	5-BURN	14-BURN	
Fall (1980)	33.1+2.0 (18)	38.0+1.6 (18)	47.1+0.9 (36)	42.0+1.3 (9)	36.9+1.4 (9)	39.4
Early Winter	32.4+0.9 (6)	35.1+1.4 (18)	37.6+1.0 (36)	36.5+1.5 (6)	29.9+1.0 (9)	34.3
Late Winter (1981)	36.7+0.8 (12)	31.3+1.2 (18)	36.2+1.0 (36)	No Data (9)	37.7+1.1 (9)	35.5
Early Spring	33.8+2.0 (12)	34.9+1.1 (18)	35.0+1.0 (36)	34.8+1.8 (6)	28.8+1.3 (9)	33.5
Late Spring	38.9+2.2 (12)	44.1+1.6 (18)	45.2+0.9 (36)	46.6+1.8 (6)	43.7+1.7 (9)	43.7
Summer	39.4+2.2 (12)	37.4+1.3 (18)	37.8+0.9 (36)	44.6+1.2 (6)	38.5+1.1 (9)	39.5
Fall (1981)	41.7+2.5 (12)	37.3+1.5 (18)	37.8+0.9 (36)	41.4+1.3 (6)	38.1+1.8 (9)	39.3
Total	36.6	36.9	39.5	41.0	36.2	

¹Control = 60 to 80 year-old spruce budworm defoliated; REC-DIST = defoliated and clearcut (CUT), and defoliated, clearcut, and burned (CUT-BURN); 5-BURN, and 14-BURN = wildfires which burned 5 and 14 years before the study began.

²Includes defoliated and clearcut (CUT), and defoliated, clearcut, and burned (CUT-BURN); does not include 5-BURN.

*Data in these columns, separated by soil type, were presented by Crawford *et al.* 1993.

BURN treatments. DDM in early winter was highest, but statistically similar, on the REC-DIST(-), 5-BURN, and DEF treatments. DDM on CONT was lower than these, but the confidence interval overlapped with DEF, 5-BURN, and 14-BURN. The 14-BURN had the lowest mean value of any treatment during this period.

Late Winter

Normally > 20 cm of snow covered all treatment types during late winter, but during this period, snow was commonly much deeper in deforested treatments (CUT, CUT-BURN, 5-BURN 14-BURN), than on forested

treatments where the overstory was intact (CONT) or where defoliated and associated mature deciduous trees remained standing (DEF) (Fig. 2). Fir and spruce use increased during this period, contributing 63% on CONT and 71% on DEF treatments. As would be expected fir use was more than 4 times that of spruce, but spruce contributed 15% and 11% of the late moose winter diet on DEF (Fig. 3) and CONT (Fig. 6) treatments, respectively, in 1981. The importance of fir and spruce decreased dramatically on the 14-BURN (Fig. 5), where deciduous species availability was greatest (Table 5). Although species were commonly eaten

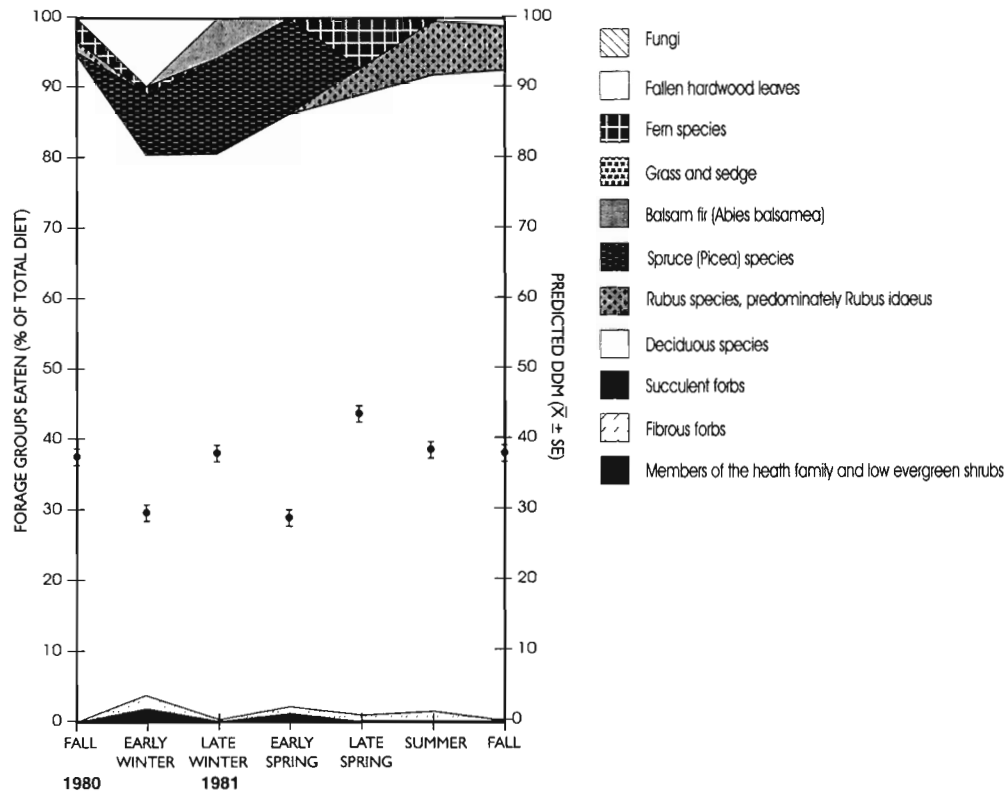


Fig. 5. Seasonal forage groups eaten (% of total diet), and predicted digestible dry matter (DDM \pm SE) on the 14-year-old wildfire (14-BURN) treatment in eastern Maine.

roughly in proportion to availability, moose selected deciduous species first, but spruce second when feeding on the 14-BURN during late winter. Selection of deciduous species is not surprising, but rejection of fir in favor of spruce seems unusual. Fir accounted for 27% of the available winter forage on the 14-BURN (Table 5), but only 5% of the late winter diet (Fig. 5). Spruce accounted 17.5% of the available forage (Table 5) but contributed 14% of the late winter diet (Fig. 5). On all but the CONT and DEF treatments, much of the low growing vegetation that would have been available at other times of the year was covered with snow (Table 5, Fig. 2) and therefore taller, early successional deciduous species became the primary forage eaten (Fig.'s 4 and 5).

During late winter, forage consumption increased significantly above the levels noted during the early winter on all treatments

(Table 3). The relatively lower consumption rate noted on the REC-DIST treatments was likely associated with the snow cover, related decreased forage availability, and associated reduced moose mobility. Snow was sometimes twice as deep in the more open deforested (CUT, CUT-BURN and 5-BURN) than in forested (DEF, CONT) treatments (Fig. 2). Although snowdepth in the 14-BURN was similar to that recorded in the REC-DIST, forage on the 14-BURN was taller, more available, and significantly more was consumed there than from any other treatment type during this feeding period.

Forage digestibility (DDM) increased significantly from the early winter means on the 14-BURN and CONT treatments (Table 6). A slight increase, over early winter values, in the use of deciduous species on both of these treatment types may have contributed to these increases (Fig.'s 5 and 6).

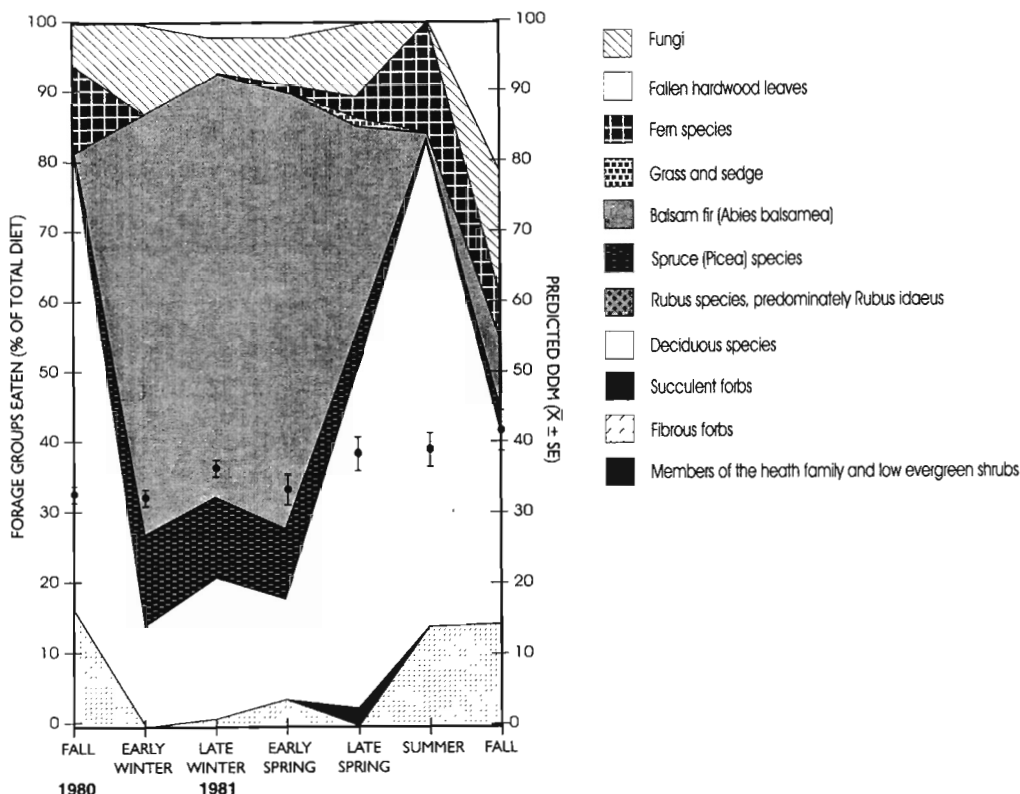


Fig. 6. Seasonal forage groups eaten (% of total diet), and predicted digestible dry matter (DDM ± SE) on control (CONT)(60-80-year-old spruce-fir forest) treatment in eastern Maine.

Mean DDM was highest and similar on CONT, REC-DIST(-), and 14-BURN plots during late winter, and significantly lower than these values on the DEF plots, probably because of the increased use of conifer forage there during this time. The 5-BURN was about 12 km from the nearest highway, and deep snow during this feeding period made access to the 5-BURN impossible. Therefore, no data were gathered there during this feeding period.

Forage selected in early spring was very similar to that selected during late winter (Fig.'s 3-6). Deciduous woody species were selected when available [REC-DIST(-), 5-BURN, 14-BURN], but where unavailable (DEF, CONT) (Table 5) conifers, primarily balsam fir, were the major forages eaten. Moose ate significantly less when feeding in CONT plots and slightly more in the DEF

plots than in the REC-DIST(-), 5-BURN and 14-BURN treatments (Table 3). With the exception of the 14-BURN, where DDM was significantly lower than it had been in late winter, and significantly lower than on the other treatment types, there were no significant differences in DDM among treatment types during this feeding period (Table 6).

Late Spring

By late spring treated plots were snow free (Fig. 2). Leaves on deciduous trees had emerged fully on deforested treatments (CUT, CUT-BURN, 5-BURN, 14-BURN) and were partly to fully emerged below overstory cover in forested treatments (CONT, DEF). Forage group use varied by treatment, but the deciduous, fern, and *Rubus* forage groups were major dietary components on all treatments (Fig.'s 3-6). Fibrous forbs and fungi

use contributed 17% and 11% of the forage consumed on DEF and CONT treatments, respectively. [Appendix I details forage consumption (% of total diet) by forage group and species, for all treatments on both soil types during this feeding period.] Moose began to strip and eat red maple bark from stump sprout clumps on deforested treatments during this feeding period. Bark, however, was never more than 2% of the wet weight of the deciduous biomass consumed.

Forage biomass consumed varied considerably among treatments during this period (Table 3). Moose ate significantly more on the 14-BURN than on other treatments, and significantly less on the CONT than on any other treatment. Forage consumption again paralleled availability (Table 5). Although a variety of forage groups were eaten, the deciduous group dominated forage choices. Increased consumption on the 14-BURN was most likely due to there being 2.5 times more deciduous forage on the 14-BURN than on REC-DIST treatments (Table 5).

Late spring diets were the most digestible (Table 6, Fig.'s 3-6) of any feeding period during the year. The 5-BURN had the highest mean DDM (46.6) during this period, but it was followed closely by DDM values on the REC-DIST(-) (CUT, CUT-BURN), the DEF, and the 14-BURN. The CONT had the lowest mean DDM (38.9), but the confidence interval for this treatment overlapped considerably with confidence intervals for the DEF and 14-BURN treatments.

Summer

Forage eaten in summer consisted primarily of leaves of deciduous species stripped from branches. In addition large quantities of foliage and fruit from *Rubus* spp., primarily *Rubus idaeus*, and maturing seed heads of grass and sedge, as well as small amounts of bark stripped from red maple and aspen clumps were eaten. Because forage was

abundant during this feeding period, moose commonly filled their needs with little movement. Although forage group selection was in many ways similar to that seen in late spring, fern and forb use decreased, while deciduous and *Rubus* spp. use increased (Fig.'s 3-6). Forage development on the CONT treatment was delayed because of overstory shading and associated competition, hence the peak in use of the deciduous forage group did not occur until summer in CONT areas (Fig. 6).

Forage consumption peaked during the summer, with a mean of 1,318g/hr (dry mass) on the 14-BURN, and 950 and 960 g/hr on the DEF and REC-DIST plots respectively (Table 3). Fungi consumption, predominantly birch conks (*Polyporus betulinus*), was relatively consistent on the control plots throughout the year except during the summer when it was not eaten (Fig. 6). Forage consumption on CONT plots during the summer was again significantly lower than on any of the other treatment types.

The CONT treatment had a slight but non-significant increase in mean DDM between late spring and summer, reflecting the delayed vegetation development, while other treatments had significant decreases (Table 6). DDM was highest on the 5-BURN, significantly higher than on any other treatment during this period. DDM on the other treatments was very similar and confidence intervals for all other treatments overlapped considerably (Table 6).

DISCUSSION

LeResche and Davis (1973) reported that tamed moose ate the same food as their wild counterparts, and foods chosen during mid-winter by wild and one of our tamed moose were very similar (Lautenschlager, unpublished). Although some may be concerned by the limited number (3) and different sexes of the moose used in this study, limited numbers and mixed sexes of tamed wild

animals have commonly been used to study the food habits of North American ungulates (Wallmo and Neff 1970, Healy 1971, Crawford 1982, Gill *et al.* 1983, Pekins and Mautz 1989, Parker *et al.* 1993), including moose (Renecker and Hudson 1985). Information presented here, as well as that by Renecker and Hudson (1992), suggest that moose eat a much broader range of forages than had previously been recognized (Peterson 1955, Peek 1974). Still, we believe Bartmann *et al.*'s (1982) advice is prudent; use caution when comparing food habits of wild and tamed wild ungulates.

Data presented here are the first available of year-round seasonal food choices, consumption rates, and associated digestibilities for moose foraging after the natural and human-caused disturbances that are common in boreal mixedwood ecosystems. Forage group availability and consumption rates varied significantly among the disturbance types examined (budworm damage, clearcutting, controlled burns, wildfires), but as noted by Renecker and Hudson (1992), consumption was closely related to availability. Although *Rubus* and fallen hardwood leaf use has been noted previously (Renecker and Hudson 1992), the use of these foods in Maine, as well as the selection of spruce during late winter, is interesting.

Like species and forage group use, consumption rates varied by treatment and season. Biomass consumption rate was lowest in early winter, increased in late winter, decreased in early spring, increased to the highest levels observed in summer, and decreased in the fall. These findings are consistent with those of Renecker and Hudson (1985, 1986). Renecker and Hudson (1985), however, present no data equivalent to our lowest (early winter) consumption period, so comparisons for that period are not possible. Moose, like deer (Silver *et al.* 1969), consume more during the growing than the dor-

mant season. Silver *et al.* (1969) reported that deer lower their metabolic rate during the winter. This study and data presented by Renecker and Hudson (1985) strongly suggest that moose do the same. Indeed, although our moose were provided dairy ration *ad libitum* throughout the year, their consumption in their pen decreased by about 1/3 during the dormant season.

Forage consumed on DEF and REC-DIST treatments throughout the year were 1.5 times greater than on CONT; however, forage consumed on 14-BURN was 2.1 times more than on CONT. Digestibility, regardless of disturbance type, had 2 statistically significant levels; "dormant season" (Nov. to Apr. = 34.4%), which included the "early spring" feeding period, and growing (May to Oct. = 40.8%). Although not statistically different, it seems that biologically the DDM within the growing season could be further divided into "late spring" (= 44%) and "late growing" ["summer" and "fall" (= 39%)] periods.

DDM was related to disturbance type only during the growing season. During the dormant season DDM was not depressed significantly by conifer (fir and spruce) consumption. Fallen hardwood leaf consumption in the fall and early winter may be an important part of a moose's diet on all treatment types, but especially in maturing or undisturbed forests. Renecker and Hudson (1985, 1992) also found that moose ate large quantities of fallen leaves during autumn. They reported leaf litter accounted for 55.6% of the Oct. diet for 1 of the 2 moose they observed, and 50-69% of the Dec.-April diet of their other moose. In addition ferns and *Rubus* spp. became a significant component of a moose's diet during the growing season in our study.

In general, the highest DDM values were observed on the most recently and/or drastically disturbed treatments, but biomass availability was reduced following the most re-

cent wildfire (5-BURN) when compared with human-caused (CUT and CUT-BURN) disturbances. Although DDM was significantly lower during the growing season on the 14-BURN, forage availability and dry matter consumption on the 14-BURN was the highest observed on any treatment type. Clearly, digestibility by itself, especially for a generalist herbivore like moose, can lead to faulty conclusions about the potential effect of treatments. Crawford *et al.* (1993) presented a broad overview of these data in terms of available digestible energy, which integrates forage: digestibility, caloric content, and availability, and reduces the potential of misinterpreting the meaning of the components presented individually.

In some ways our data are consistent with Renecker and Hudson (1985, 1988, 1992) who examined forage selection in an area with an overstory dominated by trembling aspen and balsam poplar (*Populus balsamifera*), however, our observations quantify effects on forage-related parameters following a variety of disturbance types, and we identify variability in forages eaten, consumption rates, and DDM that help put season of observation and disturbance type into perspective.

Presently there is great interest in forest management that mimics natural disturbances (Slocombe 1993, Grumbine 1994, Galindo-Leal and Bunnell 1995). In Ontario, the Crown Forest Sustainability Act (Hampton 1994) states that forest management practices should "...emulate natural disturbances and landscape patterns...". But what disturbance(s) should be mimicked, and to what degree? Should we mimic disturbance patterns, intensities, something else, or some combination? The answer depends on the specifics of interest, commonly biota, but potentially structure, and process. Determining an appropriate suite of management objectives will require identifying specifics which will likely include resources, manage-

ment practices, and ecosystems of concern (Lautenschlager 1996).

Silvicultural clearcuts and controlled burns may be less destructive [remove substantially less forest floor litter ("organic pad")] than wildfires. Consequently, "natural disturbances", like wildfires, may be slow to produce the quantity of vegetation necessary to maintain large moose populations. Our results suggest that at least in the short-term, intense wildfires may retard forest succession for several years. Forage production on our 5-BURN was limited when compared with what would have been available on a similar 5-year-old clearcut in the area. In New Brunswick moose and white-tailed deer fed most heavily on 2-year old clearcuts even though 6-year-old clearcuts produced the most forage (Telfer 1972). In Quebec, Vallée *et al.* (1976) found that forage production for moose commonly peaked 5-15 years post-harvest in the clearcuts they examined. In this study, forage production on the 5-BURN was most similar to that on our more recent, human disturbance treatments (CUT and CUT-BURN). Therefore, for analysis of forage production and consumption, we combined the 5-BURN with the more recent, 1-2-year-old, human-caused disturbances (CUT and CUT-BURN).

Cutting commonly produces an abundance of forage for moose for up to 15 years after that disturbance (Telfer 1972, Vallée *et al.* 1976). On this study area, both cutting and controlled burns led to treated areas producing an abundance of high quality forage during the growing season following treatment, and an even greater abundance 2 to 4 years following treatment (Crawford *et al.* 1993). Vegetation on controlled burn treatments suffers a temporary successional setback which may restrict the short-term production following this treatment, but that setback is not nearly as dramatic as the setback following a severe wildfire.

Our results indicate that clearcutting, a



human-caused disturbance that concerns a variety of publics (Smith 1986, Moore 1995), benefit moose more, at least in the short-term, than similar aged wildfires. When examined for available digestible energy 1 and 4 years post-treatment (Crawford *et al.* 1993), prescribed burning provided advantages greater than those provided by cutting, as suggested by Haggstrom and Kelleyhouse (1996). Although clearcuts may be managed to mimic wildfire patterns, they should not be managed to mimic wildfire intensity, if the objective is short-term moose forage production.

Longer-term consequences of cutting and wildfires are less clear. Certainly our 14-BURN produced an abundance of vegetation, nearly 600 wet g/m² 15 years after burning, but our REC-DIST treatments were producing 2/3 of this biomass 2 growing seasons after treatment. Some [discussed by Bendell (1974) and Haggstrom and Kelleyhouse (1996)] have argued that burning, by releasing nutrients, should lead to increased forage quality. In this study, forage on the 5-BURN was more digestible than forage on CUT, CUT-BURN, and the 14-BURN treatments, but forage digestibility on the REC DIST(-) during the fall of 1980 was the highest recorded during this study. This suggests that although wildfire may increase forage quality soon after the burn, controlled burning and cutting provide more biomass than similar aged wildfires, but digestibility benefits are shorter-lived on cut and controlled burn treatments. Essentially, in deforested areas, there seems to be an inverse relationship between biomass production and digestibility.

Forage produced following budworm damage (DEF) had biomass and digestible energy (kcal/ha) intermediate between CONT and CUT, and much less than that identified 4 years post-treatment on the CUT-BURN (Crawford *et al.* 1993), or on the 14-BURN during this study. Digestible energy was 2.5

and 5.6 times greater on CUT and CUT-BURN treatments, respectively, than on the DEF treatment 4 years after treatment (Crawford *et al.* 1993). Forage production increased following budworm damage, but increases are inversely proportional to the % cover of live canopy remaining in defoliated stands. Canopy cover decreases, and near-ground vegetation biomass increases, with time and continuing budworm defoliation. Budworm damage leads to a gradual overstory removal and inversely proportional increases in ground level vegetation. Therefore, forest floor decomposition and resulting nutrient releases are slower than those following treatments that remove more of the overstory at one time (cutting, wildfires); a variety of early successional plant species that become established following more severe disturbances, such as cutting, controlled burns, or wildfires, never became established following budworm defoliation. Vegetation communities that do become established following budworm damage have a low deciduous component and never develop sufficient biomass to be considered quality moose foraging habitat. The more severe disturbances (cutting, burning) remove or displace the organic pad, and open the area so that both solar radiation received and organic matter decomposition increase. These changes create a variety of microsites that are invaded by a larger number of plant species, producing larger amounts and equal or higher quality forage than would be found in areas with less severe disturbances like budworm damage.

In this paper we combined data from the 5-year-old wildfire (5-BURN) with the more recently disturbed (CUT and CUT-BURN) treatments because the vegetation on these sandy, well-drained soils required more time to regenerate following the wildfire, and forage production developed more slowly following that wildfire than on similar aged clearcut areas. Landscape-level forage di-

versity, however, may be greater following wildfires than clearcuts, particularly large cuts, because of the patchy nature of burns, and the extensive scale of these more and less intensively burned patches (Bendell 1974). In addition, budworm defoliation can create favorable moose habitat by initiating understory growth within reach of moose. Some of this is desirable moose food, while the rest is important cover. Some conifers serve as both food and cover. Like wildfire, budworm damage can create a vast mosaic and variety of vegetation types. Budworm damage commonly covers extensive areas and infestations vary in severity and duration (Blais 1985). Even when defoliation is severe, however, it is unlikely to lead to vegetation abundance, composition, or patterns similar to those found after clearcutting.

CONCLUSIONS

This study documents some effects of clearcutting, controlled burns, budworm defoliation, and wildfires on forage production and moose diets. Revegetation following budworm defoliation produced less moose forage than any of the other disturbance types examined. Wildfires retarded revegetation, so short-term forage production was reduced following this disturbance. Clearcutting and controlled burning had similar effects, producing an abundance of vegetation soon after these disturbances. Forage quality (digestibility), during the growing season, was highest on the 5-BURN, while that on the 14-BURN was very similar to that observed on the REC-DIST(-). This suggests that controlled burning is unlikely to significantly improve forage quality, and that the positive effects of disturbances such as cutting, controlled burning, and wildfires, on moose forage quality, are short-lived. Digestibility of mixed diet samples changed during the growing season, but not during the dormant (November to April) period. Digestibility ranged from 28% [early spring

(pre-leaf-out) on the 14-year-old wildfire] to 47% [fall 1980 (REC-DIST(-) and late spring (post-leaf-out) 1981 on the 5-year-old wildfire]. In this study moose ate significant amounts of food items that have been previously unobserved or considered insignificant such as fallen hardwood leaves, ferns, *Rubus* spp., and spruce (*Picea* spp.).

ACKNOWLEDGMENTS

We thank the many individuals, institutions, and agencies who helped with this study. P. O'Neil supervised site selection and initial study installation. S. Day, L. Muhlberg, S. Owens, L. Rogacki, M. Scott, R. Titterton, and W. Wright helped with study installation. S. Ahlfeld, J. Carter, A. Cobb, P. Cioffi, D. Degnen, J. Diehl, S. Finkelstein, C. George, J. Lawrence, C. Matlack, M. Olis, D. Perinne, L. Pucci, M. Ryan, P. Wayne, J. West, C. Wood, and R. Zetsch assisted with data collection, and L. Stokes performed most of the laboratory analyses. Comments from 2 anonymous reviewers, Ed Telfer, and Wendeline Price improved this manuscript significantly. USDA Natural Resource Conservation Service (formerly the Soil Conservation Service) scientists identified soils. The staff of the Moosehorn National Wildlife Refuge, USDI Fish and Wildlife Service, provided field facilities and aided in many aspects of the study. H. Haines, C. Stubbs, and R. Keys permitted us to conduct part of this study on their land. Much of this work was completed while Lautenschlager was a Ph.D. student at the University of Maine. Although part of this work was supported by the Vegetation Management Alternatives Program (VMAP) under the Sustainable Forestry Program at the Ontario Forest Research Institute, primary support was from the USDA Forest Service.

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Appendix I. Forage group composition (species) and species contribution to total diet consumption (%) during one (late spring) feeding period.

FORAGE GROUP and SPECIES LATE SPRING	CONTROL		DEFOLIATED		CUT		CUT & BURNED		WILDFIRE	
	Silty	Sandy	Silty	Sandy	Silty	Sandy	Silty	Sandy	5 - burn Sandy	14 - burn Sandy
DECIDUOUS										
American Beech (<i>Fagus grandifolia</i>)	3.2									
Beaked Hazel (<i>Corylus cornuta</i>)	3.0	40.5	14.0	0.5	28.1	3.7	15.2			15.6
Black Cherry (<i>Prunus serotina</i>)						0.4				
Bush Honeysuckle (<i>Diervilla lonicera</i>)						1.8		2.1		1.0
Fly-Honeysuckle (<i>Lonicera canadensis</i>)	0.6									
Gray Birch (<i>Betula populifolia</i>)			4.4	2.5	19.9	15.2	11.0	3.5		16.2
Hobblebush (<i>Viburnum alnifolium</i>)	0.6									
Large-toothed Aspen (<i>Populus grandidentata</i>)				1.7		3.6		14.4		3.9
Mountain Maple (<i>Acer spicatum</i>)	17.6									
Pin Cherry (<i>Prunus pensylvanica</i>)					3.8	1.5	2.9	12.7	7.1	25.1
Quaking Aspen (<i>Populus tremuloides</i>)	4.5		1.2		21.1	13.7	19.2	3.6	1.4	10.2
Red Maple (<i>Acer rubrum</i>)	13.3	8.3	7.0	10.4	3.5	7.1	5.4	4.3	0.9	1.5
Red Oak (<i>Quercus rubra</i>)			2.7							
Serviceberry (<i>Amelanchier</i> spp.)							1.2			
Speckled Alder (<i>Alnus rugosa</i>)			18.0	1.2						0.5
Staghorn Sumac (<i>Rhus typhina</i>)								0.6		
Sweet Fern (<i>Comptonia peregrina</i>)								3.7		
White Birch (<i>Betula papyrifera</i>)		4.8		16.1		4.6		3.1	11.9	4.1
Wild-raisin (<i>Viburnum Lentago</i>)	2.0					1.5				6.2
Willow spp. (<i>Salix</i> spp.)									3.5	3.7
Winterberry (<i>Ilex verticillata</i>)				4.7						
CONIFERS WITHOUT SPRUCE										
Balsam Fir (<i>Abies balsamea</i>)	32.5	18.2								
Hemlock (<i>Tsuga canadensis</i>)	8.1									
SPRUCE										
Red Spruce (<i>Picea rubens</i>)	2.5	7.2								
RUBUS										
Blackberry (<i>Rubus allegheniensis</i>)			3.5		0.6	6.3	2.4	2.2	2.5	3.6
Bristley Dewberry (<i>Rubus hispida</i>)			0.3					0.7		
Raspberry (<i>Rubus idaeus</i>)			9.5		23.1	16.0	21.3	12.9	37.3	0.5



FORAGE GROUP and SPECIES	CONTROL		DEFOLIATED		CUT		CUT & BURNED		WILDFIRE	
	Silty	Sandy	Silty	Sandy	Silty	Sandy	Silty	Sandy	5 - burn Sandy	14 - burn Sandy
HEATH FAMILY / LOW SHRUBS										
Blueberry (<i>Vaccinium</i> spp.)									0.5	
Sheep Laurel (<i>Kalmia angustifolia</i>)				1.0						
FIBROUS FORBS										
Bunchberry (<i>Cornus canadensis</i>)			1.5	3.6						
Cat-tail (<i>Typha</i> spp.)										
Clim. False Buckwheat (<i>Polygonum scandens</i>)										
Common Sarsaparilla (<i>Aralia nudicaulis</i>)			12.5	15.6			9.8	1.3		0.7
Fireweed (<i>Epilobium angustifolium</i>)										21.7
SUCCULENT FORBS										
Bluebead Lily (<i>Clintonia borealis</i>)		4.6								
False Lily-of-the-Valley (<i>Maianthemum canadense</i>)										
Strawberry spp. (<i>Fragaria</i> spp.)				0.5			0.9			
FERNS										
Bracken Fern (<i>Pteridium aquilinum</i>)			2.0	28.6			12.8	1.8	34.4	13.7
Cinnamon Fern (<i>Osmunda cinnamomea</i>)			2.0							7.2
Interrupted Fern (<i>Osmunda Claytontiana</i>)			6.5	1.3						
Sensitive Fern (<i>Onoclea sensibilis</i>)			28.2							
Unknown Fern		6.0								
SEDGE										
<i>Carex</i> spp.		1.5					1.8		9.8	
FUNGUS										
Mushrooms										21.0



FORAGE GROUP and SPECIES LATE SPRING	CONTROL		DEFOLIATED		CUT		CUT & BURNED		WILDFIRE		MEAN & STANDARD ERROR	
	Silty	Sandy	Silty	Sandy	Silty	Sandy	Silty	Sandy	5 - burn Sandy	14 - burn Sandy		
MEAN & STANDARD ERROR OF FORAGE GROUPS												
FORAGE GROUP and SPECIES LATE SPRING	Silty	Sandy	Silty	Sandy	Silty	Sandy	Silty	Sandy	Silty	Sandy	Silty	Sandy
DECIDUOUS	44.8±15.7	53.7±19.0	47.2±7.9	37.2±7.1	76.2±9.1	51.2±6.4	55.0±14.2	45.7±9.1	24.7±4.2	87.6±5.4	52.3±5.7	5.9±4.3
CONIFERS WITHOUT SPRUCE	40.7±11.0	18.2±9.4										1.0±0.7
SPRUCE	2.5±2.5	7.2±7.2										14.2±4.2
RUBUS				13.2±6.4	23.8±9.1	22.3±6.5	23.5±6.4	15.9±7.4	39.7±17.4	4.0±1.8	0.2±0.1	7.9±2.6
HEATH FAMILY / LOW SHRUB						1.0±1.0	0.5±0.5	0.5±0.5				0.6±0.4
FIBROUS FORBS	4.5±3.8		14.0±4.3	19.2±5.3		9.9±4.5	9.8±6.3	3.2±1.6	21.7±11.0	1.6±1.0		14.5±4.6
SUCCULENT FORBS	6.0±3.9		0.5±0.5			0.9±0.9						1.3±1.0
FERNS	1.5±1.5		38.8±11.5	29.8±8.1		12.8±6.1	1.8±1.8	34.6±8.6	13.8±8.3	7.2±5.0		2.1±2.1
SEDGE					1.8±1.4		9.8±6.5					
FUNGUS		21.0±13.4										