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Effects of Forest Disturbance and Soil Depth on Digestible Energy for Moose and White-Tailed Deer

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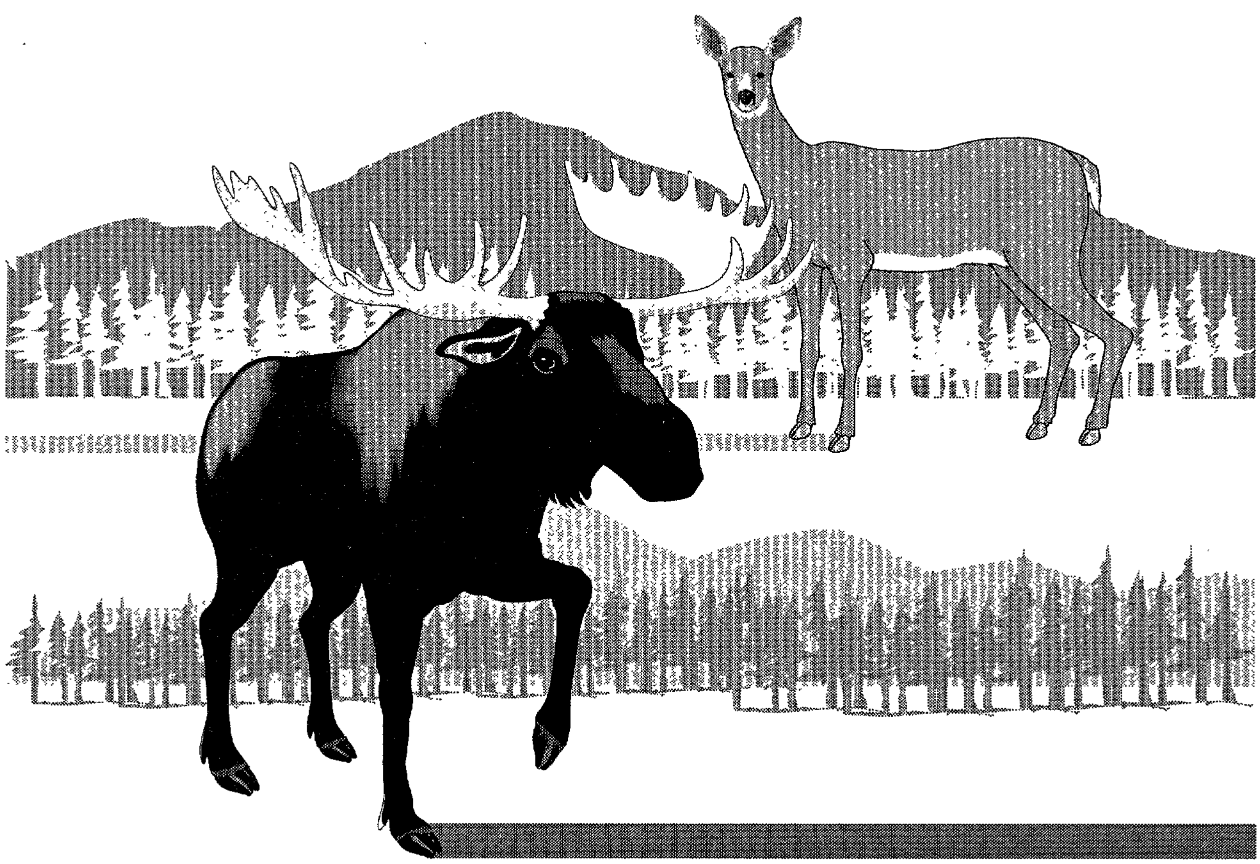

Abstract

Spruce budworm defoliation, clearcutting for salvage, and prescribed burning of clearcut areas on deep and shallow soils influenced deer and moose foraging in eastern Maine spruce-fir forests from 1980 to 1984. Plant standing crop biomass, seasonal plant selection by tractable moose and white-tailed deer, and digestible energy for deer and moose were determined for each treatment. Early successional plant species were most abundant on burned areas, and were common on clearcut areas. Increase in biomass after defoliation was substantial. Deer and moose ate many of the same plant species, but in different proportions. Deer found more desirable foods on deep than on shallow soils and were more selective of plant parts than moose. Deer digested their diets slightly better than moose from late spring through fall. Deer obtained more digestible energy than moose during fall and early winter on all treatments. Moose obtained more digestible energy than deer during spring and summer on burned areas where forage was abundant. Available energy by treatment was significantly different for moose year round and for deer during spring and fall: clearcut and burn >clearcut >defoliated >undefoliated (control).

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Introduction

Spruce budworm *(Choristoneura fumiferana)* infestations in northern coniferous ecosystems have defoliated spruce-fir (*Picea-Abies*) forests periodically for centuries (Blais 1983). These infestations often last 7 to 10 years until much of the balsam fir (*Abies balsamea*) is killed, and may progress cross-continent, covering a substantial portion of the continental spruce-fir type (Hardy et al. 1986). The outbreaks of 1910, 1940, and 1970 affected 10, 25, and 55 million ha (25, 62, and 136 million acres), respectively (Blais 1985). During severe infestations, nearly half of the spruce (*Picea glauca* and *P. rubra*) and most of the balsam fir can be killed.

The entire forest canopy can be killed over extensive areas depending on the composition of the stand. Stands suffering severe mortality contain large amounts of highly flammable fuel, which has led to severe wildfires in past infestations. Spruce budworm defoliation, by itself or in combination with wildfires or salvage cuts, sets plant succession back to early seres and modifies extensive areas of moose and deer habitat.

Within the concomitant range of white-tailed deer and moose in Canada, the most recent spruce budworm infestation occurred on approximately 54, 40, 27, 25, 30, and 31 million ha in 1975 through 1980 (Hardy et al. 1986). Defoliation solely within the range of moose approximated 18, 23, 25, 20, 14, and 14 million ha over the same period. Additionally, spruce budworm caused substantial tree mortality in Maine and Minnesota, with lesser losses reported in New Hampshire, Vermont, New York, and Michigan. Selser et al. (1985) reported dead trees on 120,000 ha and trees at severe to heavy risk on 2.2 million ha in Maine in 1983. Also, secondary insects and diseases invaded and killed weakened trees. Many trees in northern New Hampshire and northeastern Vermont were defoliated, eliminating critical winter habitat for deer.

Historically, the effects of spruce budworm defoliation, clearcutting of defoliated stands, and fire, singly and in combination, substantially modified the composition and abundance of vegetation available as food and cover for herbivores. In the most recent infestation, increased construction of logging roads and additional financial investment in forest lands resulted in greater fire-control efforts and a decrease in the area burned. As fire becomes less important as an ecological factor affecting seral stages and deer and moose habitat, will clearcutting or budworm defoliation serve the same role and benefit deer and moose habitat? Here we quantitatively describe the effect of spruce budworm defoliation, clearcutting, and fire, singly and in combination, on forage availability, forage use, and digestible energy for deer and moose.

Methods

Study Area, Plot Location, and Treatments

We established six 4- to 8-ha study blocks, three on shallow and three on deep soil on the Moosehorn National Wildlife Refuge in eastern Washington County, Maine, in 1977 through 1979. Budworm defoliation began in this area in 1974. Two undefoliated (CONTROL) blocks, one on a shallow and one on a deep soil, were established in southern Hancock County approximately 130 km southwest of the Refuge. CONTROL blocks were established in mature, 60- to 80-year-old uncut stands showing no defoliation, with three replicate plots on both shallow and deep soils. Treatment plots within blocks on the Refuge, 1 to 2 ha in size, were: defoliated but uncut (DEFOL); defoliated and all stems cut, with commercial stems removed (CUT); or defoliated and all stems cut, with commercial stems removed, followed by prescribed burning (CUTBURN). As an adjunct to help determine the longer term response of plant succession to burning, we established three plots on the Refuge in an area burned by wildfire in 1966 (14BURN).

The CONTROL as well as all stands prior to treatment were similar spruce-fir forests, approximately 60 to 80 years old, which originated after a previous budworm infestation. As in most even-aged budworm origin forests, the overstory was more than 75 percent balsam fir. Scattered pioneer hardwoods, primarily birch (*Betula papyrifera* and *B. populifolia*) and red maple (*Acer rubrum*), and shade-tolerant northern hardwoods, primarily American beech (*Fagus grandifolia*), also were present. Understory vegetation was sparse and included several fern species: *Carex* spp., *Cornus* spp., a few forbs such as *Mainanthemum canadense* and *Trientalis borealis*, balsam fir, spruce and hemlock (*Tsuga canadensis*) regeneration, and mosses.

Soils were mapped on all plots and differentiated on the basis of depth of solum. The shallow soils were mostly a Lyman-Tunbridge complex or a Tunbridge-Peru complex. Depths generally were less than 1 m, and rock outcrops were common. The deep soils were Buxton and occasional pockets of Scantic, and a Croghan-Adams complex with Adams soils on higher elevations. These soils generally were 1.5 m or more deep.

Commercially valuable trees were removed from CUT and CUTBURN plots during spring and early summer of 1979. All remaining trees larger than 2.5 cm d.b.h were cut and left on the ground during mid to late summer 1979. This residue provided copious fuel for prescribed burning. Plots were burned in May and June 1980. Strip head-fires (Crawford 1986) were used on all plots except for one ring burn.

Vegetation Sampling Techniques

Plant biomass. Standing biomass of herbaceous vegetation and woody shoots $\leq$ 1.3 cm in diameter on all plots was sampled during July-September of 1980, 1981, 1983 (burned plots only), and 1984. Biomass (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. Biomass 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 estimators were calculated for estimated weights $\leq$ 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 weight-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 weight.

After taking these measurements on the 10 temporary quadrats in each plot, it was determined randomly ($P = 0.2$) whether to clip the quadrat and record fresh and oven-dry weight of vegetation by species. Vegetation samples were collected daily 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 formulae to convert estimates to actual weights. Permanent quadrats were not clipped.

Plant selection by deer and moose. Tractable animals were reared, maintained, and trained by the techniques of Lautenschlager and Crawford (1983, 1984). They were held in pens on the Moosehorn National Wildlife Refuge, transported to the plots in a horse trailer or enclosed truck, and fed a pelleted dairy ration after returning from the plots. We observed the plants selected by two female deer (mean live weight 50 kg), and three moose (two female and one neutered male—mean live weight 300 kg). Plant selection was observed during feeding periods: summer (1 July-31 August), fall (1 September-31 October), and early winter (1 November-31 December) of 1980; late winter (1 January-19 March—moose only), early spring (20 March-30 April), late spring (1 May-30 June), summer, and fall of 1981. During each feeding period, each animal visited each treatment on each block on both shallow (12 plots) and deep soil (12 plots), as well as plots on the 14BURN block. No data were recorded during the summer of 1980 for moose and the summer and the fall of 1980 for deer; that time allows the animals to become accustomed to the area and the available foods, and for the observers to refine techniques.

Observers were trained to estimate the wet weight of plants selected by the animals and were checked for accuracy during feeding periods. Foraging was simulated by one crew member while an observer estimated its wet weight. The observer's estimated weights were later regressed against actual weights to provide a correction coefficient. Three handlers accompanied each animal to each plot for 30 minutes during each feeding trial. They estimated the wet weight by species of plants eaten in alternate bites, and collected 5- to 50-g samples of each plant eaten by the animals during every feeding trial. When possible, reproductive and vegetative parts similar to those selected by the animals were collected from the browsed plants; otherwise, similar samples were taken from nearby plants. This procedure was repeated with the remaining deer and moose until each animal had visited the plot. Animals were moved to the next plot and the procedure was repeated after allowing time for rumination and rest. When possible, we sampled two plots each morning and two each evening. Animals were allowed to move freely about plots and were redirected only if they attempted to leave a plot. The weight consumed by each animal during each 30-minute feeding period was summarized by plant species.

Plant digestibility. A representative sample of plant species eaten on each plot was oven dried at 60°C to a constant weight, 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 weight of the diet were combined to represent mixed wet-weight diets selected by deer and moose. Digestible dry matter (DDM) of mixed diets was determined with bovine rumen fluid (Crawford and Hankinson 1984) by a two-stage in vitro technique (Tilley and Terry 1963) modified by Palmer et al. (1976). Standard reference forages of known digestibility for white-tailed deer were provided by R. L. Cowan of Pennsylvania State University to convert in vitro DDM values to in vivo (Palmer and Cowan 1980) data for both deer and moose. Because no source of standard reference forages for moose were 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).

Analysis

Digestible energy available for moose and deer was calculated for each plot by multiplying forage plant biomass available by its caloric value and percent digestibility. Treatment differences in digestible energy were determined by an ANOVA with a split-plot factorial design for plots on the Moosehorn Refuge, an ANOVA with factorial to compare the CONTROL with DEFOL, and with Tukey's Studentized Range Test. Variation for the statistical analysis was determined from the values determined for digestible energy available on treatment plots. Individual values of the component parts of biomass, energy, and digestibility are presented in graphs or tables or discussed in the text. The oven-dry weight of all forage available during summer was assumed to remain available to animals until the following growing season, except when covered by snow. Leaching loss of dry matter was assumed insignificant for treatment comparisons at our latitude (45° N). Seasonal differences were not analyzed statistically because observations between seasons were not independent.

Results

Plant Biomass

We failed to detect a significant difference in plant biomass by treatment or soil depth, though probability levels were 0.07 for soil differences in 1981 and 0.06 for treatment differences in 1984. In general, biomass means for deep soils were greater than those for shallow soils, and biomass means were lowest in CONTROL and DEFOL, greater in CUT, and greatest in CUTBURN (Figs. 1-2).

On CUTBURN, *Comptonia peregrina* was by far the most abundant plant. The weight of this nitrogen-fixing species was about 1,000 kg/ha, nearly twice that of the next most abundant species on both deep and shallow soils. It also was the dominant species in 1983 and was abundant in 1981 as well, especially on shallow soils. Other abundant plants on CUTBURN in 1984 were *Populus tremuloides, Corylus cornuta, Rubus idaeus, R. allegheniensis, Pteridium aquilinum,* and *Solidago* spp. on deep soils; and *Prunus*

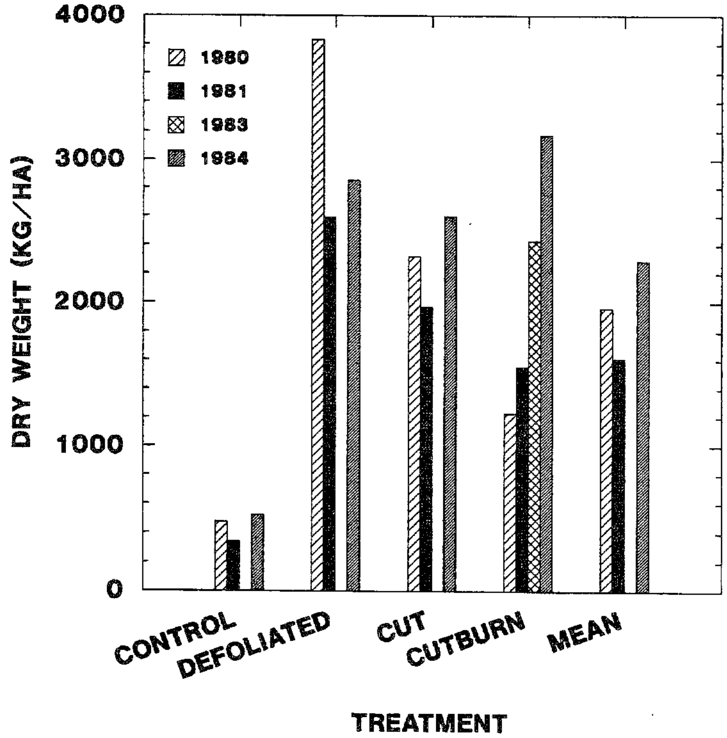

Figure 1.—Total available plant dry-weight biomass in kg/ha by treatment and year on deep soils, excluding woody stems > 1.3 cm in diameter. Only CUTBURN plots were sampled in 1983.

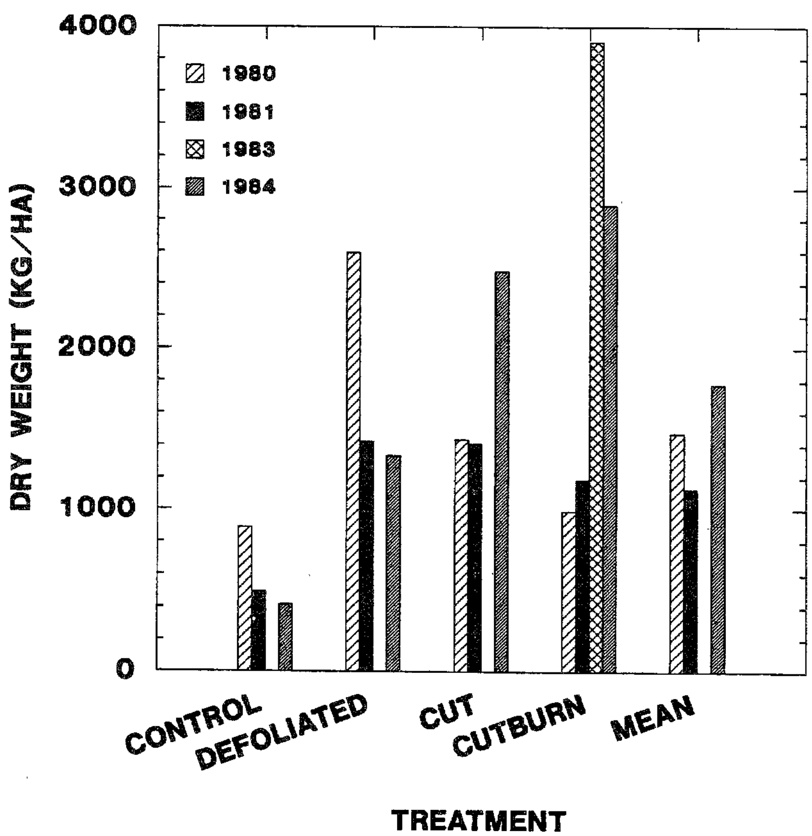

Figure 2.—Total available plant dry-weight biomass in kg/ha by treatment and year on shallow soils, excluding woody stems > 1.3 cm in diameter. Only CUTBURN plots were sampled in 1983.

pensylvanica, Populus grandidentata, P. tremuloides, Acer rubrum, and *B. papyrifera* on shallow soils.

Common plants in the CUT plots in 1984 were *Abies balsamea, R. idaeus, Pteridium aquilinum, A. rubrum,* Bryales, *P. tremuloides*, Usneaceae, and *B. papyrifera*. In 1981 on deep soils, the Bryales biomass was almost twice that of *Rubus idaeus*, the next heaviest crop. The dominance of Bryales decreased in 1984. By contrast, on shallow soils in 1984, the crop of Bryales was greater than that of any other species, increasing from 260 kg/ha in 1981 to 425 kg/ha in 1984.

On DEFOL plots, Bryales and *Abies balsamea* made up approximately 75 percent of the total on deep soils and more than 90 percent on shallow soils. These plants were abundant in the understory prior to defoliation and had responded substantially by 1980 to almost 6 years of gradual overstory defoliation. More species of plants were found by 1984 but mosses and fir were still the most abundant groups on shallow and deep soils. In 1984, other important species were Usneaceae, *R. idaeus* and *R. allegheniensis*, and *A. rubrum.*

Mosses made up more than 75 percent by weight of the total vegetation on CONTROL. These are normal year-to-year fluctuations in the understory of dense *Picea-Abies* stands.

Plants Eaten

Deer. Deer ate deciduous woody species more often year round than any other group of foods. Forbs were the second most common year-round food group, followed by lichens; the semiwoody genus *Rubus*; grasses, sedges, and rushes; fallen hardwood leaves; ferns; conifers; fungi; members of the heath family and low evergreen shrubs; and mosses. Foods eaten varied seasonally and by treatment and soils (Table 1).

Deer ate more species of plants, and usually greater quantities of each of these species, on deep soils than on shallow soils. This was true for all treatments but less pronounced in CUT plots.

On CUTBURN deep-soil plots, more *Carex* spp. biomass was eaten than that of any other species. It was the plant eaten most during early and late spring and also was eaten throughout summer and fall. *Prunus pensylvanica* and *Rubus* spp. were readily eaten from early spring through early winter. *Salix* spp. was eaten from late spring through fall. Consumption of *Carex* spp. was less on shallow soils but was an important food during early and late spring. Deer ate more woody plants on shallow soils than on deep soils. *P. pensylvanica* was the primary food on these plots. *Carex* spp. was consumed more on deep than on shallow soils of the CUT treatment, with most use occurring during spring. Consumption of woody plants and *Rubus* spp. was not substantially different between deep and shallow soils for this treatment.

The deeper soils of CONTROL plots provided a richer herbaceous flora as food than shallow soils. Here, deer ate forbs such as *Maianthemum canadense, Trientalis borealis, Clintonia borealis, Aster* spp., and grasses. By contrast, deer depended more on woody plants for food on shallow soils. In DEFOL stands where budworm had defoliated *Abies* and *Picea* but the rest of the overstory remained intact, *M. canadense* was eaten more than any other species on both deep and shallow soils. This species provided deer with succulent growth shortly after snowmelt. Its leaves and fruits were eaten throughout summer, and the cured plant was consumed into fall. *T. borealis* and *C. borealis* were eaten in spring, summer, fall, and early winter, but in slightly lesser amounts than *M. canadense*. Aster shoots, flowers, and basal leaves were consumed during summer and fall. Grasses, largely *Poa canadensis*, were eaten during spring, summer, and fall. Mixed fallen hardwood leaves and fungi were important foods in stands with a hardwood overstory, regardless of soil depth. The inclusion of fungi in a mixed diet with fallen hardwood leaves enables deer to digest the energy-rich leaves (Crawford 1982).

Moose. Moose also ate more deciduous woody plants year round than any other food (Table 2). *Abies balsamea, Rubus* spp., ferns, *Picea*, mixed fallen hardwood leaves, fungi, forbs, heath and low evergreen shrubs, grasses, and sedges also were eaten. As with deer, foods selected varied by season, treatment, and soils.

Differences in plant consumption by soil type were not as great for moose as for deer. In CONTROL plots, *Picea* and *Abies* were eaten often in winter and spring but less in summer and fall. In DEFOL plots these same species were eaten most during winter and early spring. *Abies* was eaten to a greater extent than *Picea*, but the latter was readily selected during those seasons. *P. rubens* was the most common species of *Picea*. It has not been considered as readily eaten by moose. *P. glauca* also was consumed but to a lesser extent than *P. rubens*. In the sparse understory of the shallow soil CONTROL plots, moose ate considerable quantities of fungi, including gilled and bracket fungus. Fungi was not often eaten in DEFOL plots, but *Pteridium aquilinum* and *Aralia nudicaulis* were, especially in shallow-soil areas. Deciduous woody plants as a group were eaten more than any other food on all plots with a woody canopy.

Differences in food selection between soil types were not important on CUTBURN and CUT treatments for moose. Deciduous woody plants such as *Acer rubrum, Populus tremuloides, P. grandidentata, P. pensylvanica, Betula papyrifera* and *B. populifolia, Cornus cornuta, Rubus* spp., and ferns, especially *P. aquilinum*, were eaten frequently.

Plant Digestibility by Deer and Moose

The dry-matter digestibility of mixed diets selected by deer (Table 3) and moose (Table 4) varied somewhat by soil depth and treatment but varied more with season. Digestibility of mixed diets by deer was low in early spring, increased to a peak in late spring and summer, then declined throughout the rest of the year. Digestibility of mixed diets by moose was low in early spring, increased in late spring, decreased in summer on all treatments except the control, increased during fall on cut areas, and declined through winter. Deer appeared to digest their diets slightly better than moose, particularly from late spring through fall.

Table 1.—Green weight (in grams) of plants eaten by two deer on each treatment and deep (DS) and shallow (SE) soils during summer 1981 feeding trails

Family or species	Control		Defoliated		Cut		Cut-burned		Percent of total
	DS	SS	DS	SS	DS	SS	DS	SS	
Acer rubrum	39	14	35	66	35	44	34	31	2.8
Alnus rugosa	3	–	37	–	25	1	–	–	0.6
Amelanchier spp.	2	8	23	26	14	21	4	–	0.9
Aster spp.	30	–	26	–	5	11	20	4	0.9
Betula papyrifera	26	20	83	216	55	85	23	87	5.6
Betula populifolia	–	27	60	90	90	176	47	15	4.8
Bryales	3	42	–	1	4	2	–	–	0.5
Carex spp.	22	37	26	10	121	39	22	62	5.1
Clintonia borealis	35	–	–	23	–	1	–	–	0.6
Cornus spp.	72	315	53	41	9	14	36	37	5.4
Corylus cornuta	5	281	225	8	66	1	43	–	5.9
Diervilla lonicera	–	3	23	1	25	29	28	82	1.8
Erechtites hieracifolia	–	–	2	3	6	9	37	8	0.6
Fragaria virginiana	–	3	3	–	42	3	14	–	0.6
Fungus	45	149	1	11	1	6	19	3	2.2
Graminiae	19	4	10	–	41	22	61	5	1.5
Leaves, fallen hardwood	73	88	13	11	6	5	6	5	1.9
Lichen	146	40	138	161	46	56	7	–	5.6
Lonicera canadensis	15	60	8	–	–	–	–	–	0.8
Maianthemum canadense	267	10	228	309	22	101	2	10	8.9
Populus grandidentata	–	–	–	44	15	69	10	109	2.3
Populus tremuloides	64	–	23	24	45	105	65	39	3.4
Potentilla simplex	–	–	–	–	14	–	49	–	0.6
Prunus pensylvanica	–	–	71	8	109	154	175	348	8.1
Prunus serotina	–	2	17	5	14	–	19	2	0.6
Pteridium aquilinum	3	5	4	58	18	30	32	81	2.1
Quercus rubra	65	16	89	–	12	–	1	–	1.7
Rubus allegheniensis	–	–	16	7	96	24	78	47	2.5
Rubus idaeus	–	1	134	24	176	176	139	96	7.0
Salix spp.	–	–	–	–	46	74	91	–	2.0
Solidago spp.	–	–	4	–	23	15	17	12	0.7
Trientalis borealis	67	1	106	65	–	3	–	–	2.3
Vaccinium spp.	–	–	1	6	1	31	31	12	0.8
Veronica officinalis	–	152	4	1	37	2	7	–	1.9
Viburnum spp.	6	5	54	28	36	65	20	1	2.0
								Total	95.0[a]

[a] Total is < 100 percent because only plants ≥ 0.5 percent of total are included.

Errata

In the headings above Tables 1 and 2 on Pages 5 and 6, respectively, the designation for shallow soils should be **(SS)**.

Table 2.—Green weight (in grams) of plants eaten by three moose on each treatment and deep (DS) and shallow (SE) soils during summer 1981 feeding trials

Family or species	Control		Defoliated		Cut		Cut-burned		Percent of total
	DS	SS	DS	SS	DS	SS	DS	SS	
Abies balsamea	1506	2274	3064	1728	192	50	2	–	5.1
Acer rubrum	1718	873	2670	3645	3949	5740	2422	2078	13.3
Acer spicatum	1125	–	–	291	–	–	–	–	0.8
Alnus rugosa	3	–	1930	–	162	171	16	–	1.3
Aralia nudicaulis	193	–	1045	2803	203	6	–	5	2.4
Betula papyrifera	202	70	534	7187	480	1680	86	1914	7.0
Betula populifolia	9	53	1800	1119	1051	1751	350	356	3.7
Carex spp.	10	–	–	–	106	177	1473	123	1.1
Comptonia peregrina	–	–	–	631	348	175	880	1330	1.9
Cornus spp.	70	604	239	178	19	70	260	48	0.9
Corylus cornuta	122	3470	4998	112	2484	–	1379	4	7.2
Diervilla lonicera	–	–	–	–	181	869	195	1258	1.4
Epilobium angustifolium	–	–	2	171	293	805	–	9	0.7
Fagus grandifolia	1056	–	6	7	–	–	–	–	0.6
Fungus	–	2980	23	10	–	–	38	–	1.8
Ilex verticillata	–	–	233	1729	–	7	–	–	1.1
Onoclea sensibilis	8	129	1072	301	6	159	–	–	1.0
Osmunda claytoniana	285	87	2119	107	4	66	–	–	1.5
Picea rubens	426	328	631	536	–	–	–	–	1.1
Polygonum scandens	–	–	–	–	12	481	661	348	0.9
Populus grandidentata	12	–	–	567	44	1245	6	7704	5.5
Populus tremuloides	613	–	161	98	2152	3046	2102	595	5.0
Prunus pensylvanica	–	–	679	361	1352	1619	1423	6765	7.0
Quercus rubra	26	35	1719	–	179	–	–	–	1.1
Rubus allegheniensis	–	–	378	57	643	603	594	397	1.5
Rubus idaeus	1	–	2752	707	3695	2566	3861	1518	8.7
Salix spp.	–	–	5	–	155	488	216	17	0.5
Tsuga canadensis	669	–	–	232	–	–	–	17	0.5
								Total	84.6[a]

[a] Total is < 100 percent because only plants ≥ 0.5 percent of total are included.

Table 3.—Mean percent digestible dry matter (standard error) of deer mixed diets by treatment, deep (DS) and shallow (SS) soils, and season

Treatment	Early spring	Late spring	Summer	Fall	Early winter
Control					
DS	26(1.2)	55(7.1)	46(3.8)	40(1.4)	[a]
SS	40(3.7)	51(2.6)	48(1.1)	38(2.6)	[a]
Defoliated					
DS	32(1.2)	52(3.7)	53(2.3)	43(2.1)	42(5.6)
SS	28(1.8)	51(4.7)	52(3.6)	39(2.4)	30(3.0)
Cut-unburned					
DS	39(1.2)	53(4.7)	51(1.9)	50(3.2)	35(1.1)
SS	34(1.9)	57(5.6)	43(1.4)	40(1.8)	37(3.1)
Cut-burned					
DS	48(2.5)	57(4.6)	47(3.3)	45(1.1)	42(3.3)
SS	43(4.4)	60(2.8)	49(2.8)	36(2.3)	42(3.9)

[a] Unsampled.

Table 4.—Mean percent digestible dry matter (standard error) of moose mixed diets by treatment, deep (DS) and shallow (SS) soils, and season

Treatment	Early spring	Late spring	Summer	Fall	Early winter	Late winter
Control						
DS	33(1.9)	43(2.7)	41(2.3)	35(1.9)	[a]	36(1.4)
SS	35(2.4)	35(2.5)	38(2.7)	38(2.1)	32(0.9)	33(0.8)
Defoliated						
DS	36(2.0)	46(1.7)	37(2.4)	42(0.9)	34(1.7)	28(1.6)
SS	34(0.9)	42(2.5)	37(1.0)	34(1.4)	36(2.3)	35(1.2)
Cut-unburned						
DS	30(1.0)	45(0.8)	35(1.4)	43(1.4)	36(1.2)	36(2.9)
SS	36(0.8)	45(1.8)	42(1.7)	42(1.1)	36(0.8)	36(0.9
Cut-burned						
DS	37(3.0)	46(1.4)	36(1.6)	44(1.5)	39(2.6)	35(2.6)
SS	36(1.8)	45(2.6)	38(1.4)	40(2.5)	38(2.6)	37(0.7)

[a] Unsampled.

Digestible Energy

Digestible energy available for deer and moose increased from 1981 (the first full growing season following treatment) to 1984 (Fig. 3) on all disturbance treatments and corresponded with an increase in biomass from 1981 to 1984 (Figs. 1-2). By contrast, there was little difference in digestible energy from 1981 to 1984 on CONTROL. An ANOVA that used only temporary plots to assure independence of observations showed a significant difference in available digestible energy ($P < 0.05$) between 1981 and 1984 for moose but not for deer. Digestible energy values for CUTBURN in 1983 were slightly less than those in 1984, approximately 62,000 and 67,000 for deer and moose, respectively.

With respect to season, digestible energy available for deer differed little from early spring through fall on CUT (Fig. 4) and CUTBURN (Fig. 5) in 1981. On DEFOL (Fig. 6), more digestible energy was available for deer during summer. On CONTROL (Fig. 7), deer obtained more energy during fall than during the growing season. By 1984, digestible energy available for deer on all treatments except DEFOL generally was as high as or higher during fall and early winter than during the growing season. By contrast, energy available to moose did not increase during the dormant season in either year and generally was highest during periods of active plant growth.

CUTBURN areas had the most digestible energy available for deer and moose, followed in decreasing order by CUT, DEFOL, and CONTROL (Fig. 3). These relationships were similar in 1981 and 1984. Treatment differences for moose were significant ($P < 0.05$) in all seasons; for deer, the treatment differences were significant ($P < 0.05$) only during fall in 1981 and in early spring, late spring, and fall of 1984. Early winter was not tested for deer because the number of samples taken during this season was insufficient for statistical analyses.

Treatment differences were more pronounced in 1984 than in 1981. For deer, the available energy in DEFOL was more than twice that of CONTROL, CUT was twice as great as DEFOL, and CUTBURN was nearly twice that of CUT (Fig. 3). These differences were approximately the same for moose in 1984 except for DEFOL, which had nearly 10 times more available energy than CONTROL (Fig. 3). In DEFOL areas, more energy was available for moose on deep soils than on shallow soils for both 1981 and 1984. Differences due to soil depth were not significantly different ($P < 0.05$) on the other treatments except for CUTBURN in early spring of 1981.

We failed to detect significant differences ($P < 0.05$) in energy available for deer vs. moose except for the spring of 1981. However, our data means indicate that more digestible energy was available for deer than for moose during all seasons in

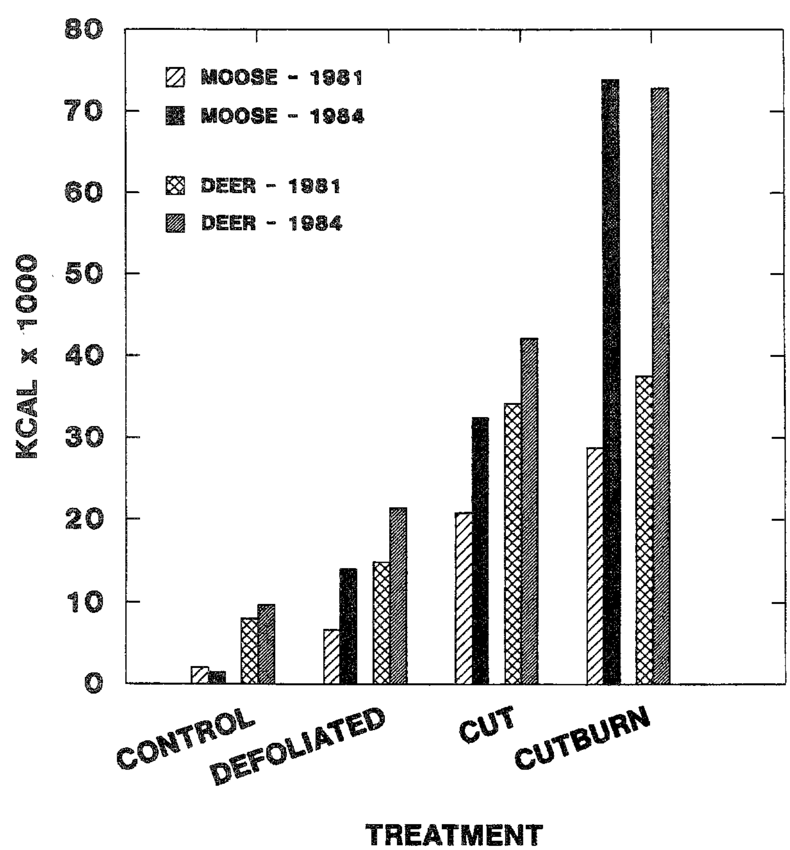

Figure 3.—Digestible energy in kcal/ha (X1000) available for deer and moose by treatment and year.

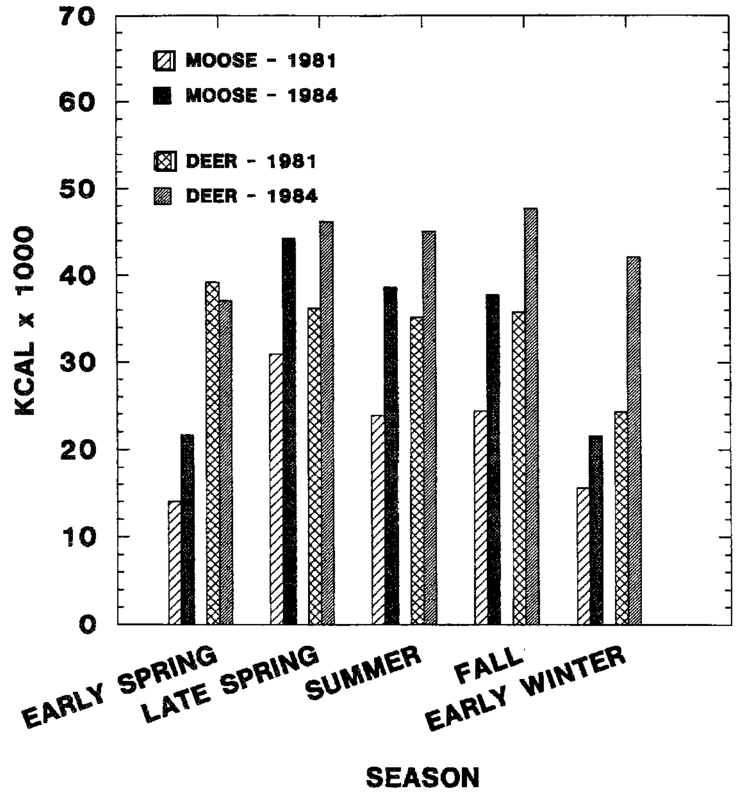

Figure 4.—Digestible energy in kcal/ha (X1000) available for deer and moose on CUT plots by season in 1981 and 1984.

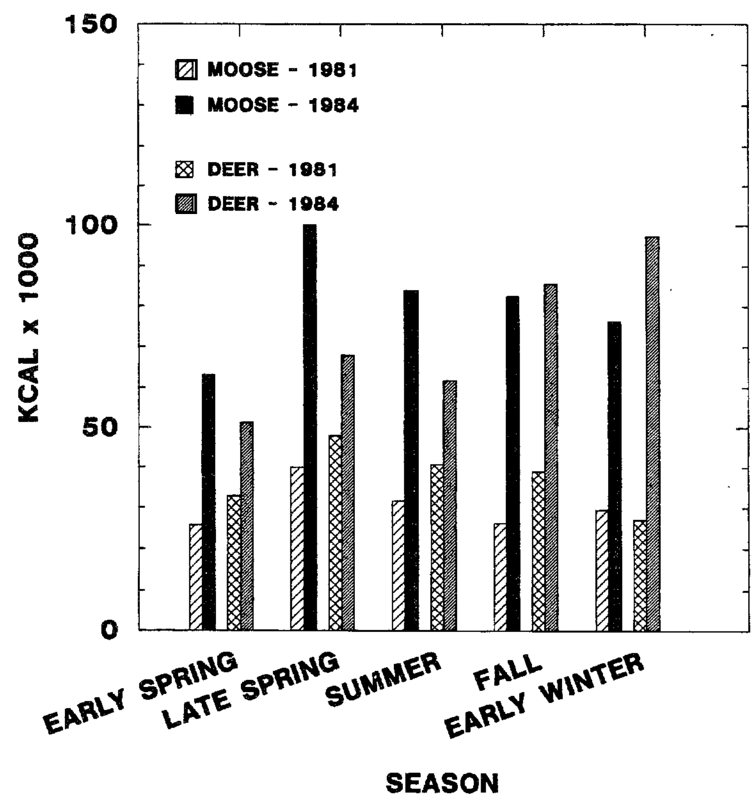

Figure 5.—Digestible energy in kcal/ha (X1000) available for deer and moose on CUTBURN plots by season in 1981 and 1984.

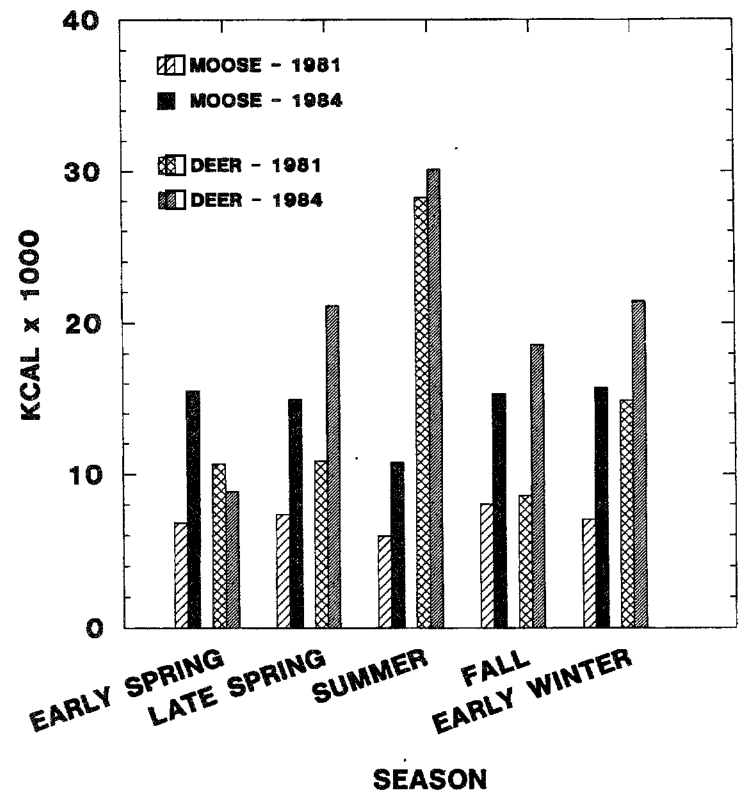

Figure 6.—Digestible energy in kcal/ha (X1000) available for deer and moose on DEFOL plots by season in 1981 and 1984.

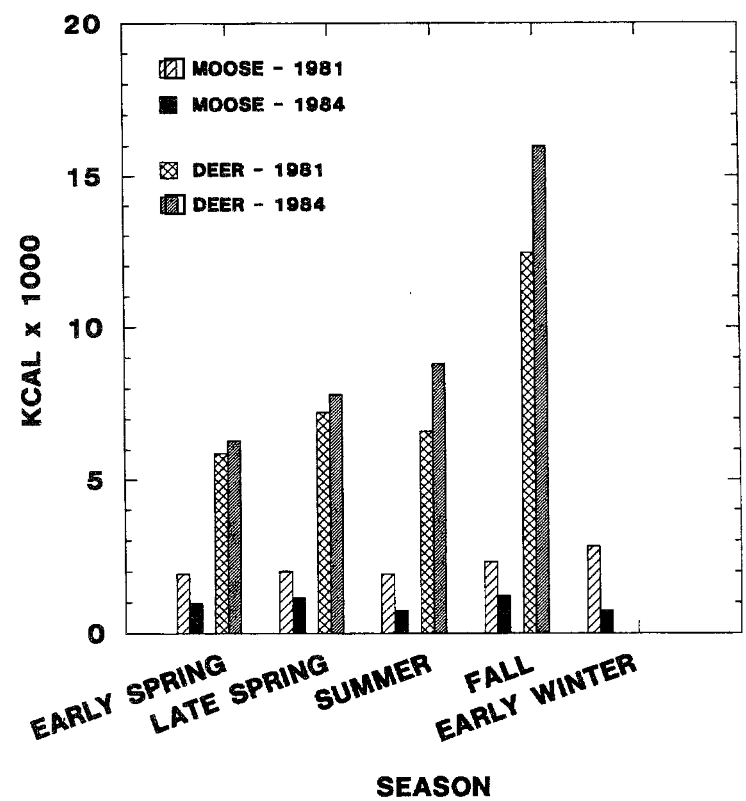

Figure 7.—Digestible energy in kcal/ha (X1000) available for deer and moose on CONTROL plots by season in 1981 and 1984.

1981 except for early winter in CUTBURN. More energy appeared to be available for deer than for moose during the fall and early winter of 1984 on all treatments.

Discussion

Several conditions that existed during this study determine how reliably our results can be extrapolated. The same two deer were not used throughout the study. The use of different animals likely caused greater variation in food selection than would have been the case if the same two animals were used for the entire study. This variation increased the residual variance of the ANOVA and made the test for deer more conservative, because we were less likely to reject a null hypothesis when it was false (type II error). In the case where we failed to detect a significant increase in digestive energy from 1981 to 1984 for deer, we suspect that there may be a true difference, especially for CUTBURN. This implies that treatment effect may be longer lasting than our statistical analysis indicates. However, we also assumed that foods eaten in 1981 were the same foods eaten in 1984. This could have reduced the residual variance of the ANOVA except that the variation in foods eaten within year was as great as the variation between years and likely would not cause treatment bias.

Also, we failed to detect significant differences in the amount of digestible energy for deer between treatments in all seasons. We did detect this treatment difference for some seasons for deer and all seasons for moose. We hypothesize that the difference is true for all seasons and that all treatment differences are real.

Likewise, where the greater amount of digestible energy available for deer than moose tested insignificant, we hypothesize that there is a true difference. Deer and moose ate many of the same species (Tables 1-2) but we observed that deer were more selective of plant parts eaten than moose. Deer nipped twig ends and buds and seldom ate the more fibrous thicker cell-wall proximal portions of the twigs, as did moose. Fibrous and thick cell-wall tissues require more time to chew and decrease food intake (Crawford and Whelan 1973; Spalinger et al. 1986). Deer frequently would take a plant in their mouth and then reject it; moose seldom did this. Also, deer were more selective of foods growing on deeper soils, which generally offer better conditions for plant growth—more digestible cell material. Moose selected plants or plant parts which appeared less digestible than those selected by deer (Tables 3-4).

Large amounts of available energy consumed by deer during fall and early winter prepare the animals for late winter (Crawford 1982). Moose moved and searched for food in snow that would restrict the movement of deer. However, the foods moose found during winter were low in digestible dry matter. Thus, even though deer movement is restricted by snow during winter, the apparent physical advantage of larger size in moose may be offset by the ability of deer to select more digestible portions of energy-rich foods prior to deep snowfall. Such adaptability is influenced by: (1) the greater maneuverability of a smaller animal, which enables it to find desirable plant portions, and (2) the ability to pick small, more digestible parts because of smaller mouth size. However, during periods of rapid plant growth during spring and summer, a greater amount of the plant is digestible and moose compete more favorably with deer for energy because of their greater capacity and need to ingest large quantities of forage. Apparently, deer are more efficient energy consumers than moose during periods of plant dormancy or where acceptable biomass is limited. Our data show that biomass accepted as food is substantially more abundant after burning than it is following defoliation or clearcutting. Wickstrom et al. (1984) indicated that deer are more efficient harvesters than elk when acceptable biomass is limiting.

While periodic defoliations by spruce budworm increase the amount of digestible energy available for moose and deer, this increase is far more substantial if the infestation is followed by clearcutting for salvage and burning. Cutting is more likely to follow defoliation today and in the future than in the past because balsam fir has increased in value through the years. However, the same increase in value plus today's more intensive forest management—including improved fire control—make it less likely that fire will have much effect on future habitats.

Our data (Fig. 3) indicate that burning benefits moose and deer equally. However, deer appear to gain more digestible energy than moose from defoliation and clearcutting.

While burning initially provides more digestible energy than other treatments, this effect may not last long. The amount of digestible energy available 3 years after burning (1983) (Figs. 8-9) was nearly as great as in 1984, indicating that treatment effect may have been at a maximum in 1984. Digestible energy available on plots burned by wildfire 15 to 17 years ago was substantially lower than yields 3 to 4 years after burning.

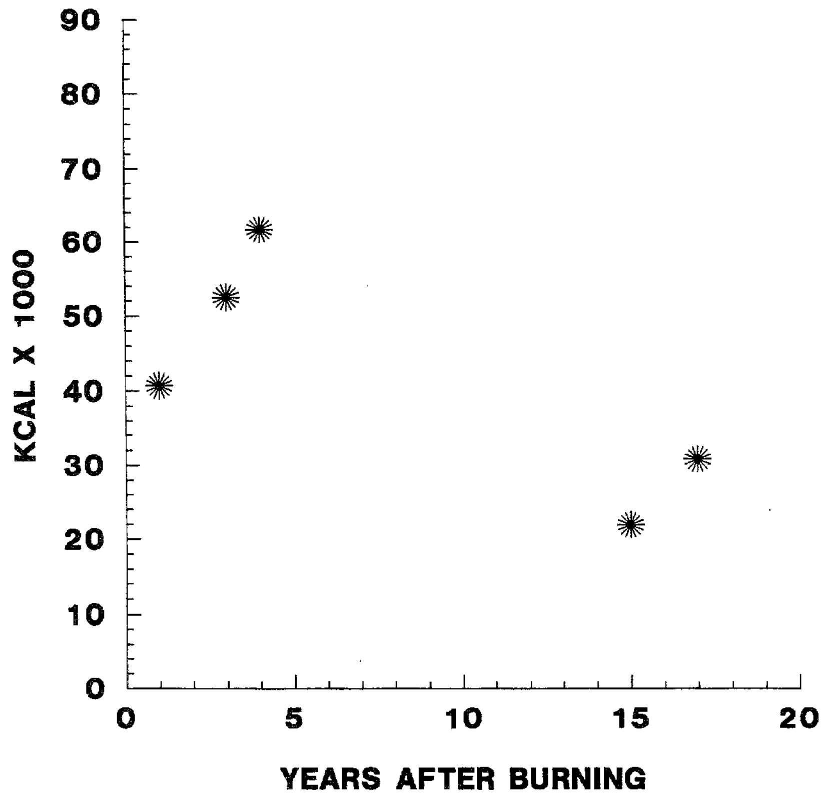

Figure 8.—Mean digestible energy during summer available for deer after burning.

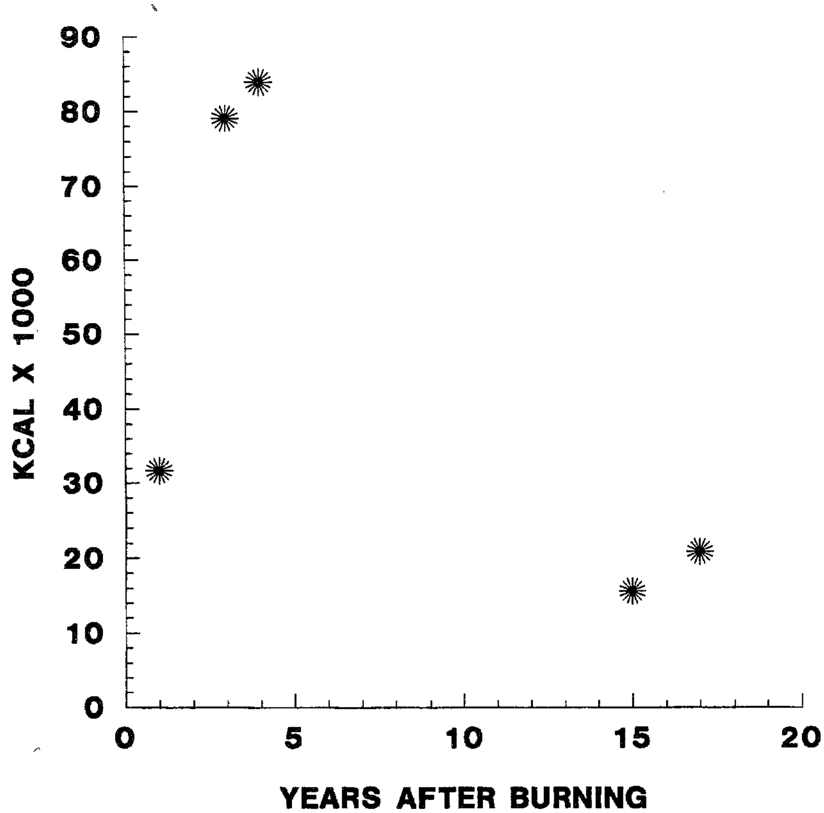

Figure 9.—Mean digestible energy during summer available for moose after burning.

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Crawford, Hewlette S.; Lautenschlager, R. A.; Stokes, Martin R.; Stone, Timothy L. 1993. **Effects of forest disturbance and soil depth on digestible energy for moose and white-tailed deer.** Res. Pap. NE-682. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 13 p.

Spruce budworm defoliation, clearcutting for salvage, and prescribed burning of clearcut areas on deep and shallow soils influenced deer and moose foraging in eastern Maine spruce-fir forests from 1980 to 1984. Plant standing crop biomass, seasonal plant selection by tractable moose and white-tailed deer, and digestible energy for deer and moose were determined for each treatment. Increase in biomass after defoliation was substantial. Deer and moose ate many of the same species, but in different proportions. Seasonal production of available energy by treatment was significantly different for moose year round and for deer during spring and fall: clearcut and burn > clearcut > defoliated > undefoliated (control).

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