WINTER FORAGING ECOLOGY OF MOOSE ON GLYPHOSATE-TREATED CLEARCUTS IN MAINE

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Abstract: The herbicide glyphosate is widely used in northern coniferous forests of the United States and Canada to promote conifer dominance on clearcut sites by suppressing regeneration of deciduous species. We determined effects of glyphosate treatment of regenerating clearcuts on (1) browse availability (total biomass, by species, and proportion with high digestible energy [DE] content), (2) browse use, and (3) diet quality of moose *(Alces alces)* in winter in Maine during 2 periods: 1-2 and 7-11 years posttreatment. We measured browse availability and use and collected browse samples for nutritional analyses on 12 clearcuts in January-March 1991 before aerial treatment with glyphosate of 6 of these clearcuts in August 1991. We conducted posttreatment sampling of treated and untreated clearcuts during January-March 1992 and 1993. We also sampled 14 clearcuts that had been treated with glyphosate 7-11 years earlier and 5 untreated clearcuts of similar age in January-March 1992 or 1993. Available biomass (kg/ha) of deciduous browse decreased $(P = 0.001)$ 70% on treated clearcuts relative to untreated clearcuts from pretreatment to year 2, but was not affected $(P = 0.29)$ at 7-11 years posttreatment. Available browse from red maple *(Acer rubrum)* and paper birch *(Betula papyrifera)* appeared to decrease less than pin cherry *(Prunus pensylvanica)* in years 1-2 suggesting that species composition on sites may influence the magnitude of effects on total browse availability. The proportion of deciduous browse biomass with a relatively high DE content (1.8 kcal/g) was not affected $(P = 0.37)$ by treatment at 1-2 years, but was greater $(P = 0.047)$ on treated than untreated clearcuts at 7-11 years posttreatment. Biomass and percent of available deciduous browse eaten by moose were not affected $(P > 0.1)$ by glyphosate in years 1-2, but were 4-5 times greater $(P < 0.1)$ on treated than untreated clearcuts at 7-11 years posttreatment. The DE and protein content of moose diets on clearcuts was not affected $(P > 0.1)$ by treatment in either time period. Initial reductions in browse availability may decrease the suitability of clearcuts for foraging by moose, but this effect would decrease over the next 5-9 years because browse availability decreases naturally on untreated sites. We concluded that glyphosate did not have important effects on diet quality. Heavy browsing in older treated clearcuts suggests that moose may be attracted to these sites, but this behavior was not directly related to browse availability or nutrition. We discuss management options for minimizing effects of glyphosate treatment on moose habitat.

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Herbicides are widely used for managing forest vegetation in northern coniferous forests of the United States and Canada (McCormack 1994). A total of 217,825 ha in Canada was treated with herbicides in 1988, the majority in central and eastern provinces, and 81% of treatment was with glyphosate (Campbell 1990). In Maine, 13,000-35,000 ha were treated annually from 1987 to 1992 (McCormack 1994) with an estimated 80% by aerial application of glyphosate (M. L. McCormack, Jr., pers. commun.). Glyphosate is used on naturally regenerating clearcuts or young plantations to promote production of conifer crop trees by suppressing regeneration of deciduous vegetation. After harvest, rapidly growing deciduous trees and shrubs shade and suppress growth of regenerating conifer trees (Newton et al. 1992a). Reduced competition from deciduous cover after treatment increases growth and survival of conifers (Newton et al. 1992b). Toxic effects of glyphosate on wildlife are minimal (Atkinson 1984), but short-term effects on habitat can be significant (Morrison and Meslow 1983).

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Regenerating clearcuts are preferred foraging habitat for moose in winter because of the abundance of deciduous browse on these sites (Peek et al. 1976, Telfer 1978, Monthey 1984). Several published studies have quantified reductions in winter browse availability 1-2 years after glyphosate treatment (Connor and McMillan 1988, Cumming 1989, Newton et al. 1989), but the magnitude of reported effects varied. Glyphosate application rates, forest site types, and site preparation methods varied greatly among these studies and likely account for some of the variation in effects on browse. Small sample sizes (*n* = 2-4 sites/treatment group) in these studies also limited statistical analyses. In the only long-term study, Newton et al. (1989) concluded that herbicide-treated sites contained more available browse than untreated sites at 9 years posttreatment because crowns of deciduous saplings in untreated sites had grown out of reach (>2.5 m) of moose. However, this response depended on the herbicide type and application rate. These authors proposed that herbicide treatment could improve long-term foraging conditions for moose by extending the period of browse availability after timber harvest.

Reductions in browse availability 1-2 years after glyphosate use may reduce foraging efficiency of moose or carrying capacity of moose habitat. Glyphosate efficacy also varies among deciduous species (Pitt et al. 1992), which may influence site-specific effects on total browse availability and the relative availability of high and low value browse species. No studies have examined effects of glyphosate treatment on browse availability relative to nutritional quality or examined effects on diet quality of moose. Our objectives were to determine effects of glyphosate treatment of regenerating clearcuts in Maine on: (1) browse availability (total biomass, species, and proportion with high DE), (2) browse use, and (3) diet quality of moose in winter in Maine during 2 time periods, 1-2 and 7-11 years posttreatment.

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STUDY AREA

The study was conducted in northern Somerset and Piscataquis counties, Maine. Forests in the region are managed for timber production. Clearcuts, partial harvests, regenerating stands, and older second-growth stands predominate the area. Forests are classified as spruce (*Picea* spp.)-balsam fir (*Abies balsamea*)-northern hardwoods (Westvald et al. 1956). Abundant tree species on regenerating clearcuts include paper birch, pin cherry, red maple, aspen (*Populus tremuloides* and *P. grandidentata*), red spruce (*Picea rubens*), and balsam fir. White pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), striped maple (*A. pensylvanicum*), sugar maple (*A. saccharum*), yellow birch (*B. alleghaniensis*), mountain ash (*Sorbus americana*), and willow (*Salix* spp.) also were common. Plant nomenclature follows McMahon et al. (1990). During our study moose were abundant in the region (1.2-1.8/km^2: Maine Dep. Inland Fish, and Wildl., unpubl. data).

METHODS

Study Design

We selected 12 clearcuts dominated by deciduous regeneration (1-3 m tall) to study effects of glyphosate at 1-2 years posttreatment. Clearcuts were 18-89 ha in area, harvested 4.5-8.5 years before treatment, and had tall (>12 m) conifer or mixed conifer-deciduous forest around at least 75% of their perimeters. Clearcuts were widely distributed (75 km between furthest sites; no sites were juxtaposed) and located in the vicinity of Moosehead Lake, Maine (Table 1). We sampled browse availability and use on all 12 clearcuts during January-March 1991 before glyphosate treatment of 6 clearcuts in August 1991. We conducted posttreatment sampling during January-March 1992 and 1993. We paired clearcuts according to vegetation, age,

Table 1. Number of clearcuts, years since timber harvest, and years since treatment for clearcuts used to study effects of glyphosate treatment on moose activity and habitat at 1 and 2 years and 7-11 years posttreatment in northern Maine, January-March 1991-93. Clearcuts used to study 1-2 year effects were treated in August 1991 after pretreatment sampling in January-March 1991.

			Years since harvest as of January 1992		Years since treatment as of January 1992	
Time period/location	Treatment	No. of clearcuts	*1*	Range		Range
1-2 years						
Moosehead Lake area	Treated	6	6.3	5.5-8.5	0.3	0.3
Moosehead Lake area	Untreated	6	5.3	4.5-6.5		
7-11 years						
Moosehead Lake area	Treated	6	15.8	13-18	7.3	6.5-9.5
Telos area	Treated	8	13.8	12-18	8.0	6.5-8.5
Moosehead Lake area	Untreated	5	19.4	16-22		

and location to reduce variation between treatment and control clearcuts, and we randomly assigned 1 clearcut from each pair to receive a single application of glyphosate (1.65 kg acid equivalents/ha). Sites were treated by helicopter by Scott Paper Company.

We used 19 clearcuts to study effects of glyphosate at 7-11 years posttreatment (Table 1). Clearcuts were 16-73 ha in area and had tall conifer or mixed conifer-deciduous cover around at least 75% of their perimeters. Fourteen of the 19 clearcuts had received a single aerial application (1.65 kg acid equivalents/ha) of glyphosate 6.5-9.5 years before initial sampling (1992). Six clearcuts were located in the Moosehead Lake area, and 8 clearcuts were located about 40 km to the northeast in the Telos area. The 5 other clearcuts, all located in the Moosehead Lake area, had not been treated. Mean age since harvest for these 5 untreated clearcuts (*x* = 19 yr) was greater than treated clearcuts in Moosehead Lake (*x* = 16 yr) and Telos (*x* = 14 yr) areas. This increased the likelihood that we would observe greater browse availability on treated than untreated sites as reported by Newton et al. (1989) because deciduous trees had longer to grow beyond the reach of moose on untreated sites. We measured browse availability and use a single time on these 19 clearcuts during January-March 1992 or 1993.

Browse Availability and Use

We counted live twigs (browsed and unbrowsed) of deciduous browse species on 1- x 5-m quadrats randomly located on transects distributed systematically on each clearcut. We sampled 24 quadrats per clearcut in 1991 and 40 per clearcut in 1992 and 1993. The 12 younger clearcuts were sampled each year, and the 19 older clearcuts were sampled in either 1992 or 1993. We defined available browse for each year as current annual growth (CAG) twigs >5 cm in length plus previously browsed CAG twigs all in a 0.5-3.0 m height stratum (Crete and Jordan 1982). Deciduous browse included paper birch, pin cherry, aspen, red maple, yellow birch, striped maple, sugar maple, mountain maple *(Acer spicatum),* willow, and mountain ash. Available browse biomass (kg/ha) was calculated by multiplying counts of browsed and unbrowsed twigs by average dry mass of twigs for each species. We determined average twig mass for young clearcuts and older clearcuts separately, but averaged across treatments because glyphosate did not affect mean twig biomass on sites (K. S. Raymond, unpubl. data). We estimated available biomass (kg/ha) of balsam fir browse by determining mean dry mass of browse (CAG 5: 5 cm and in a 0.5-3.0 m height stratum) on trees in each of 4 height classes (0.5-1.0, 1.1-2.0, 2.1-3.0, >3.0 m) and multiplying these means by counts of trees in each height class in quadrats. We measured mean browse biomass per tree for 30-60 trees per height class equally distributed among treatment groups.

We estimated biomass (kg/ha) of deciduous and balsam fir biomass eaten by moose by measuring twig diameters at point of browsing by species and converting diameter measurements to twig mass using twig diameter-mass regressions. Diameter-mass regressions were based on samples of 150-642 twigs per species and had R^z values of 0.76 to 0.92 (Raymond 1994). Sampling dates were evenly distributed during January-March with mean sampling dates in mid-February. Because moose probably feed on woody twigs from November to May in Maine, our estimates of browse biomass use account for about one-half of the period of woody browse use. Percent use was calculated by dividing biomass used by biomass available.

Browse and Diet Quality

We conducted nutritional analyses on a composite sample of each browse species on each clearcut in 1991 and 1992. Because we saw little variation in nutritional quality values of individual species within and among treatment groups and years (K.S. Raymond, unpubl. data), we used corresponding mean values for treatment groups from 1991 to 1992 in 1993 for diet quality analyses. Composite samples consisted of all CAG from 12 randomly selected stems. We kept samples frozen until they were freeze-dried and analyzed for fiber composition (Mould and Bobbins 1981), percent nitrogen (Williams 1984), percent tannin by the radial diffusion method (Hagerman 1987), and gross energy. We multiplied percent nitrogen by 6.25 to estimate crude protein. We calculated DE content (kcal/g) based on fiber composition, crude protein, and tannin using an equation developed for white-tailed deer *(Odocoileus virginianus)* (Robbins et al. 1987a,fc) and recommended for large cervids (Hanley et al. 1992). To use this equation, we converted percent tannin data determined from the radial diffusion method to bovine serum albumin precipitating equivalents by regression (Hagerman 1987).

We examined browse availability relative to nutritional quality using the method of Hobbs and Swift (1985). In this analysis, forage biomass available at a specified diet quality level is calculated by cumulative addition of forage biomass in decreasing order of forage quality. Using this method, we calculated the available biomass of deciduous browse at a specified DE content of 1.8 kcal/g for each clearcut. This value was at the upper quartile of the range of DE values for deciduous browse species on our sites (Raymond 1994). We then calculated the proportion of available browse on clearcuts with a mean DE content of 1.8 kcal/g. We omitted balsam fir from this analysis because its exceptionally high availability would mask effects on deciduous browse, and its use by moose was low. We calculated the DE and protein content of browse biomass eaten by moose on each clearcut from browse use (kg/ha) and nutritional quality data at the species level. We first measured fiber composition, protein, and tannin, and calculated DE of samples of each browse species clipped at average-diameter-at-point-of-browsing. We analyzed subsamples of each of the same composite samples described above for these browse quality measurements. We calculated only dietary DE and protein for clearcuts with >2% (25% of overall mean use) use of available deciduous browse because percent use of browse species (diet composition) was highly variable when total browse use on clearcuts was low.

Statistical Analyses

Availability, use, and diet quality data were not normally distributed; therefore, we used analysis of variance (ANOVA) on ranks (Zar 1984:176). We tested effects at 1-2 years for treatment and year using a 2-factor repeated-measures ANOVA. Because there was a pre-treatment year, a year by treatment interaction was evidence for a treatment effect. Therefore, P values for treatment effects are for the year x treatment interaction unless noted otherwise. We tested effects at 7-11 years posttreatment using a 1-factor ANOVA. In this case, P values refer to main effects. Before this analysis, we tested for area differences between treated clearcuts in the Moosehead Lake and Telos areas. When area differences were found, we excluded data from the Telos area because all other sites were in the Moosehead Lake area. We used an alpha level of 0.10 to reduce the probability of a type II error (failure to reject the null hypothesis of no effect from glyphosate treatment when it is false).

RESULTS

Browse Availability and Use

1-2-Year Effects.—Mean browse biomass (across years and treatments) ranged from 41 to 192 kg/ha for total deciduous browse (Fig. 1). Paper birch, pin cherry, aspen, and red maple composed 88-93% of deciduous browse on untreated clearcuts each year (Fig. 2), but yellow birch, striped maple, sugar maple, mountain maple, willow and mountain ash also occurred (Raymond 1994). Deciduous browse biomass decreased ($P < 0.001$) on treated clearcuts compared to untreated clearcuts (Fig. 1.). Deciduous browse biomass on treated clearcuts was 30% (58 kg/ha) less than on untreated clearcuts by year 1 and 70% (96 kg/ha) less by year 2. Paper birch, pin cherry, and red maple browse biomass decreased (P < 0.01) 63-94% from pretreatment to year 2 and was 67-88% less than on untreated clearcuts at year 2 (Fig. 2, Table 2). Availability of aspen exhibited a similar trend, but was not statistically different (P = 0.103). Balsam fir browse biomass ranged from 100 to 419 kg/ha and was not affected (P = 0.23) by treatment (Fig. 1).

Mean percent use of deciduous browse by moose ranged from 5 to 13% across years and treatments (Fig. 3); however, this estimate was made at the midpoint in the period for moose use of woody browse and potentially represents one-half of total use. Use of balsam fir was low (<1%). Treatment did not affect (P > 0.10) the percentage or biomass of total deciduous browse eaten by moose (Table 2). However, mean biomass of deciduous browse used exhibited a decreasing trend similar to browse availability whereas percent browse used on treated and untreated clearcuts was similar, suggesting that total deciduous biomass used by moose was reduced by treatment.

7-11-Year Effects—Biomass of total deciduous browse, 3 of 4 common deciduous species (aspen was the exception), and balsam fir browse did not differ (P > 0.10) between Moosehead Lake and Telos areas for treated clearcuts (Raymond 1994); therefore, we pooled data from these areas for statistical analyses. Total deciduous browse biomass did not differ (P = 0.29) between treated (44 kg/ha) and untreated (47 kg/ha) clearcuts (Fig. 1). Red maple and paper birch were consistently abundant on clearcuts, and biomass did not differ (P = 0.3-0.8) between treated and untreated sites (Fig. 4). Biomass of willow and aspen was greater (P = 0.01-0.05) on treated clearcuts, and biomass of mountain maple, striped maple, and yellow birch was greater (P = 0.01-0.05) on untreated clearcuts (Table 2). Balsam fir browse was abundant and 2 times greater *(P* = 0.02) on treated (3,656 kg/ha) than untreated clearcuts (1,690 kg/ha) (Fig. 1). Percent use of deciduous browse differed (P = 0.04) between older treated clearcuts in the Moosehead Lake (21%) and Telos areas (5%). Moose track and bed data collected on these clearcuts in a concurrent study also indicated there was less moose activity on clearcuts in the Telos area (Eschholz 1993). Therefore, we only included use data from the Moosehead Lake area in these analyses because all untreated sites were in that area. Percent use of deciduous browse was greater (P = 0.036) on treated *(x*= 21%) than untreated *(x*= 4%) clearcuts (Fig 3). Percent use of balsam fir was low for both treatments (<0.3%).

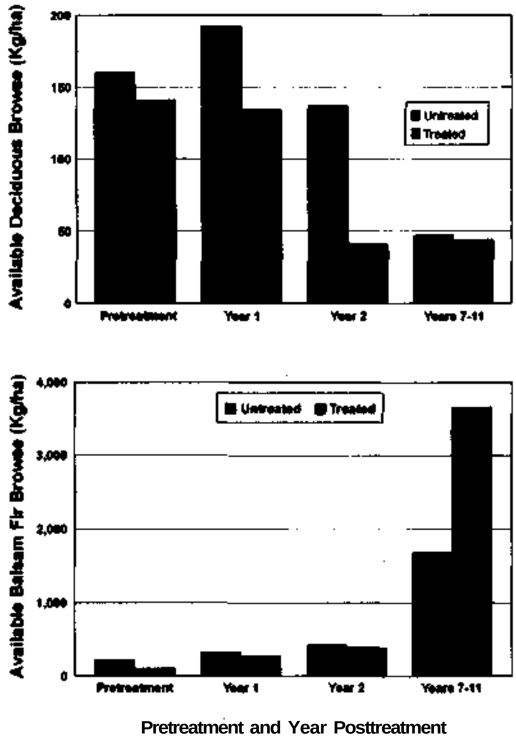

Fig. 1. Availability of deciduous and balsam fir browse on glyphosate-treated and untreated clearcuts at pretreatment and 1, 2, and 7-11 years posttreatment in Maine, January-March 1991-93. Clearcuts used to study 1-2 year effects were treated in August 1991 after pretreatment sampling in January-March 1991.

Browse and Diet Quality

The proportion of deciduous browse biomass with a cumulative mean DE content of 1.8 kcal/g was not affected (P = 0.37) by treatment at 1-2 years, and mean proportions were similar for both treatments and years (Fig. 5). At 7-11 years posttreatment, treated sites had a greater (P = 0.047) proportion of biomass at a cumulative mean DE content of 1.8 kcal/g ($x \pm$ SE = 0.43 ± 0.10, n = 14) than untreated clearcuts ($x \pm$ SE = 0.06 ± 0.03, n = 5). The greater proportion on treated clearcuts was largely the result of greater availability of willow and aspen, which had greater DE than most other deciduous species (Raymond 1994). The DE and protein content of moose diets and the decid-

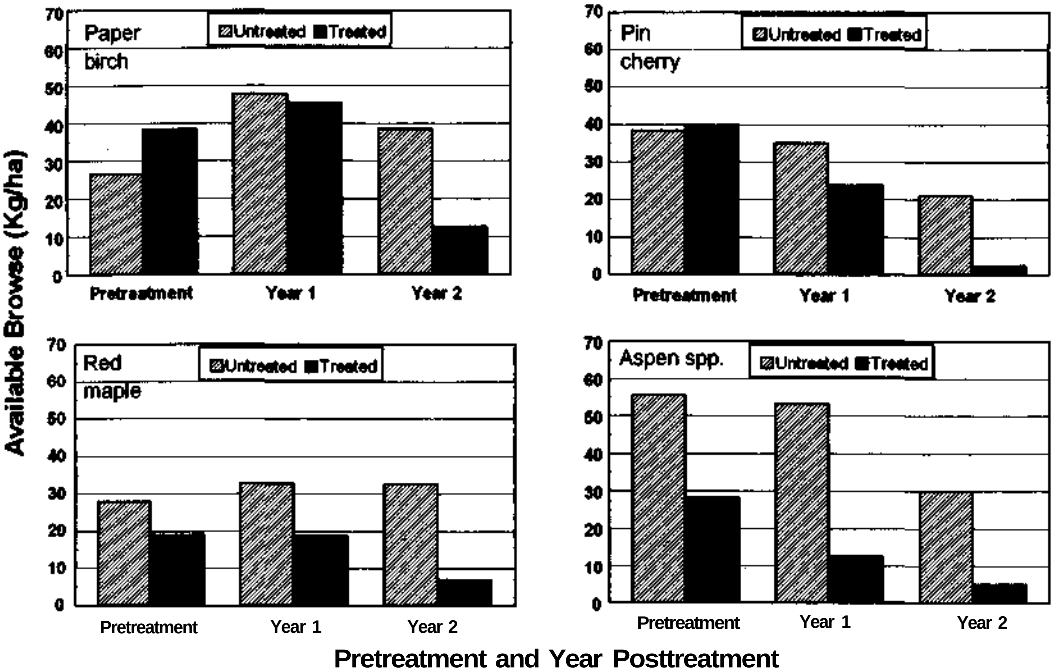

Fig. 2. Available browse from 4 common deciduous species on glyphosate-treated and untreated clearcuts from pretreatment to year 2 posttreatment in Maine, January-March 1991-93. Clearcuts used to study 1-2 year effects were treated in August 1991 after pretreatment sampling in January-March 1991.

uous component of moose diets varied little from a nutritional perspective and were not affected ($P > 0.10$) by treatment in years 1-2 or 7-11 (Table 3). Mean dietary DE values tended to be slightly greater in years and treatments in which the biomass of balsam fir eaten by moose was relatively high because balsam fir has a high DE (2.45 kcal/g: Raymond 1994).

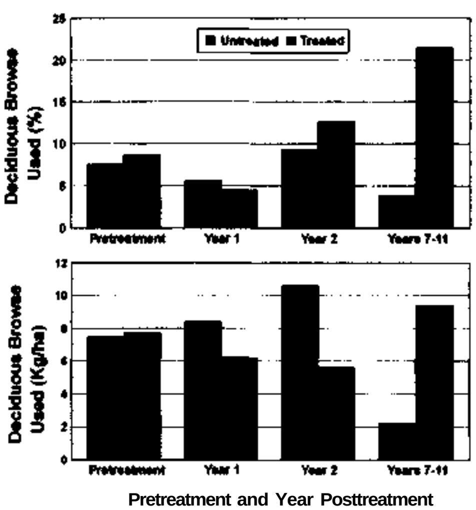

Fig. 3. Biomass and percentage of available deciduous browse eaten by moose on glyphosate-treated and untreated clearcuts at pretreatment and 1, 2, and 7-11 years posttreatment. Clearcuts used to study 1-2 year effects were treated in August 1991 after pretreatment sampling in January-March 1991.

DISCUSSION

1-2-Year Effects

The treatments were silviculturally effective, and the 70% decrease in deciduous browse biomass we observed during the second winter after treatment was in the range of values reported in other studies (Connor and McMillan 1988, Gumming 1989, Newton et al. 1989). The first winter after treatment, much of the deciduous vegetation exhibited signs of glyphosate injury (e.g., color and morphological changes), but only 25% of deciduous stems were dead (lack of a green cambium) (Eschholz 1993) as has been observed elsewhere (Connor and McMillan 1988). Mortality from glyphosate results from chronic inhibition of several metabolic processes including protein synthesis and secondary compound formation (Cole 1984) and is probably delayed by winter dormancy. We saw no evidence that moose avoided feeding on injured plants during the first winter after treatment.

Table 2. Summary of effects of glyphosate treatment of regenerating clearcuts on browse availability, use, and digestible energy content and diet quality of moose at 2 time periods after treatment. Numbers in parentheses are *P* values for treatment effects or relative differences for means of treated clearcuts compared to untreated clearcuts.

	1-2 years posttreatment	7-11 years posttreatment
Deciduous browse availability (kg/ha)		
Total deciduous	decrease ($P < 0.001$) (70%)[1]	NS[2] ($P = 0.289$)
Red maple	decrease ($P < 0.001$)	NS ($P = 0.793$)
Paper birch	decrease ($P < 0.001$)	NS ($P = 0.333$)
Pin cherry	decrease ($P = 0.010$)	NS ($P = 0.982$)
Aspen	NS ($P = 0.103$)	increase ($P = 0.053$)
Willow		increase ($P = 0.014$)
Mountain maple		decrease ($P = 0.009$)
Striped maple		decrease ($P = 0.033$)
Yellow birch		decrease ($P = 0.054$)
Balsam fir	NS	increase ($P = 0.017$)
Proportion deciduous browse biomass with mean DE = 1.8 kcal/g	NS ($P = 0.368$)	increase ($P = 0.047$) (7x)
Deciduous browse use		
Biomass	NS ($P = 0.147$)	increase ($P = 0.045$) (4x)
Percent	NS ($P = 0.236$)	increase ($P = 0.036$) (5x)
Nutritional quality of total browse diets eaten by moose on clearcuts		
Digestible energy	NS ($P = 0.140$)	NS ($P = 0.936$)
Protein	NS ($P = 0.704$)	NS ($P = 0.523$)

[1] Differences between means are for yr 2 posttreatment.
[2] Not statistically different at $P < 0.10$.

Similar percent use values for treated and untreated clearcuts in year 1 suggested that avoidance of injured plants did not occur; however, low use rates on injured twigs may have been offset by greater use rates in small patches missed by treatment (Santillo 1994). We did not study the nutritional quality of injured browse during year 1 (although injured twigs were included in random sampling of browse), but DE, protein, and tannin content of browse from injured plants in year 2 differed little from untreated plants except that current annual growth of treated plants was smaller in some species (Raymond 1994).

Glyphosate efficacy on pin cherry and aspen is high (Stasiack et al. 1991) and greater than for paper birch and red maple (Pitt et al, 1992), a trend we also observed in our browse data. Browse reductions were 94, 82, 69, 63% for aspen, pin cherry, paper birch, and red maple, respectively, in the present study although the

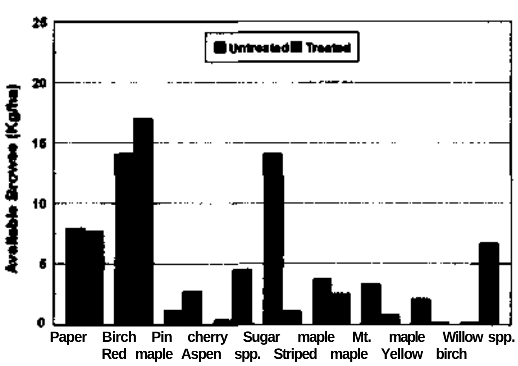

Fig. 4. Available browse from common deciduous species on glyphosate-treated and untreated clearcuts at 7-11 years posttreatment in Maine, January-March 1992-93.

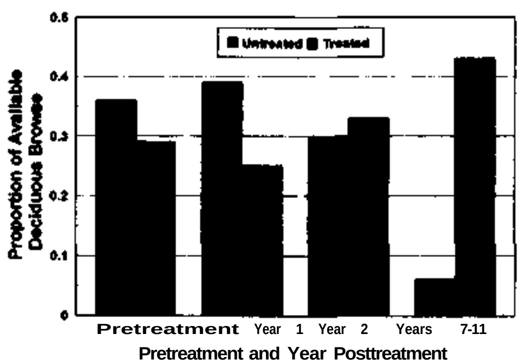

Fig. 5. Proportion of available deciduous browse biomass with relatively high digestible energy content (1.8 kcal/g) for glyphosate-treated and untreated clearcuts at pretreatment and 1, 2, and 7-11 years posttreatment. Clearcuts used to study 1-2 year effects were treated in August 1991 after pretreatment sampling in January-March 1991.

Table 3. Digestible energy (kcal/g) and protein (%) content of total browse biomass (includes balsam fir) and deciduous browse biomass eaten by moose in glyphosate-treated and untreated clearcuts in Maine, January-March 1991-93[1]. Clearcuts used to study 1-2 year effects were treated in August 1991 after pretreatment sampling in January-March 1991.

	Pretreatment and 1-2 years posttreatment									7-11 years posttreatment					
	Pretreatment			Year 1			Year 2			Moosehead Lake area			Telos area		
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE
Digestible energy															
Treated															
Total diet	5	1.67	0.07	3	1.67	0.06	6	1.81	0.08	5	1.59	0.01	5	1.76	0.16
Decid. diet	5	1.67	0.07	3	1.59	0.01	6	1.59	0.04	5	1.57	0.01	5	1.62	0.05
Untreated															
Total diet	4	1.83	0.16	5	1.63	0.06	5	1.55	0.02	3	1.71	0.20			
Decid. diet	4	1.58	0.07	5	1.58	0.07	5	1.54	0.02	3	1.47	0.02			
Protein															
Treated															
Total diet	5	5.72	0.18	3	5.70	0.04	6	5.77	0.32	5	4.94	0.15	5	5.33	0.28
Decid. diet	5	5.72	0.18	3	5.68	0.06	6	5.59	0.33	5	4.91	0.15	5	5.18	0.22
Untreated															
Total diet	4	5.91	0.44	5	5.53	0.17	5	5.52	0.12	3	5.62	0.61			
Decid. diet	4	5.63	0.41	5	5.46	0.20	5	5.50	0.14	3	5.14	0.31			

[1] Only clearcuts with >2% use of total deciduous browse were included.

effect on aspen was not statistically significant. Relative differences in efficacy among these abundant species may influence the magnitude of glyphosate effects on individual clearcuts. For example, clearcuts dominated by pin cherry and/or aspen would have greater proportional reductions in browse availability than clearcuts dominated by paper birch or red maple. Low use of balsam fir despite its abundance suggested that it was avoided on our clearcuts as found in other studies where deciduous browse was abundant (Telfer 1967, McNicol and Gilbert 1980, Thompson et al. 1989).

7-11-Year Effects

Newton et al. (1989) concluded that herbicides increase deciduous browse availability for herbivores at 9 years posttreatment, but for glyphosate applied at a rate of 1.65 kg/ha Newton et al. (1989) and this study found no difference in deciduous cover or browse biomass in 1.0-2.5 or 0.5-3.0 m height strata, respectively. Our untreated clearcuts were 3 years older on average than our treated clearcuts (19 vs. 16 yr) which may have masked a small negative effect on browse availability because more browse may have grown out of reach of moose on the older untreated sites. In contrast to Newton et al. (1989), we did not find that nearly all browse had grown out of reach of moose on our untreated clearcuts. We suggest that results of these 2 studies differed because we used large entire clearcuts as experimental units as opposed to the 1-ha study plots in a single clearcut used by Newton et al. (1989). Treatment and control plots in Newton et al. (1989) were initially placed in parts of their clearcut study area that had relatively uniform regeneration for the purpose of studying herbicide efficacy (M. L. McCormack, Jr., pers. commun.). Vegetation in large clearcuts is typically patchy, and areas with little deciduous regeneration initially may take longer than 9 years to grow entirely out of the reach of moose. Also on 2 of our untreated clearcuts, heavy browsing and stem breakage by moose had maintained a substantial density of deciduous stems <3.0 m tall.

Moose were probably eating more than 50% of the actual usable browse on older treated sites because our use estimate (21%) was for one-half of the winter period, and moose ate only an average of 60% of the biomass of individual twigs (K. S. Raymond, unpubl. data), which effectively lowers actual availability. This heavy browsing may influence future browse availability by slowing vertical growth of deciduous stems on treated clearcuts and prolonging the period of browse availability (Bergurud and Manuel 1968, Hjeljord and Gronvold 1988).

Based on rates of browse use, older treated clearcuts appeared to receive the most intensive use by moose, but this did not appear to be a response to food availability or quality. Deciduous browse availability did not differ between treated and untreated clearcuts. The proportion of deciduous browse biomass with a cumulative

DE content of 1.8 kcal/g was greater on older treated clearcuts, but mean DE of deciduous browse eaten by moose (i.e., diets) was similar on treated (1.57 kcal/g) and untreated (1.47 kcal/g) clearcuts and similar to the overall mean DE of available deciduous biomass (1.54 kcal/g) suggesting that there was not strong selection for browses with higher DE content. Eschholz et al. (1996) hypothesized that greater foraging activity on older treated clearcuts was due to greater conifer cover for bedding and/or protection from winter weather.

Implications for Moose Foraging

Several lines of evidence indicate that moose did not browse more intensely on treated clearcuts in year 2 to compensate for reduced browse availability. Moose used similar proportions of deciduous browse on treated and untreated clearcuts and did not increase use of balsam fir. Average bite size (diam at point of browsing) of the 4 common deciduous browse species also did not differ between treated and untreated clearcuts in year 2 (K. S. Raymond, unpubl. data). However, negative trends for treatment effects on moose track counts (Connor and McMillan 1988, Eschholz et al. 1996) and biomass of deciduous browse used suggest that moose used treated clearcuts less as a result of lower average browse density or lower density of suitable foraging patches.

We assessed effects of treatment on the potential for 40-ha clearcuts to provide deciduous browse for moose overwinter (150 days). Forty-ha clearcuts are common in Maine and reported sizes of moose activity centers in Maine and Ontario range from 25 to 52 ha (Thompson and Vukelich 1981, Thompson 1987). At pretreatment, deciduous browse availability on our clearcuts averaged 90 kg/ha and treated clearcuts in year 2 and treated and untreated clearcuts in years 7-11 had an average of 26 kg/ha after adjusting for the average proportion (0.6) of twig weight at mean diameter-of-point-of-browsing (K. S. Raymond, unpubl. data). Based on a daily browse intake of 4.6 kg per day, calculated from a dietary DE of 1.6 kcal/g (this study), and a daily DE requirement for a 350 kg moose experiencing a 20% weight loss overwinter (Schwartz et al. 1988), young untreated clearcuts had sufficient browse to support 5.2 moose per 40 ha compared to 1.5 moose for treated sites at both time periods. These are probably overestimates of forage-based-carrying-capacity, but values near 1 for treated clearcuts suggest that clearcuts of this size do not have sufficient deciduous browse to solely support individual moose over winter. Because moose use several activity centers within large winter home ranges (Thompson and Vukelich 1981), effects of glyphosate use on local populations will ultimately depend on the number and distribution of alternative foraging areas. Moose also could increase use of balsam fir, as fir is frequently reported in the diet of moose in areas where deciduous availability is low (Peek 1974). Moose apparently can subsist on diets with high proportions of balsam fir; however, avoidance of fir in our study area suggests such a foraging shift would represent a decline in diet quality because conifers contain substantial secondary compounds (Bobbins et al. 1987a).

MANAGEMENT IMPLICATIONS

We found little evidence that glyphosate treatment had significant negative effects on diet quality of moose; therefore, habitat management for moose can focus on maintaining adequate browse availability at the landscape level. The basic strategy would be to reduce long-term fluctuations in browse availability for moose populations by managing the number and location of treated and untreated clearcuts on the landscape. Effects of treatment on browse availability may be most pronounced when all similar-aged clearcuts in a locality are treated simultaneously to achieve cost efficiency from a central helicopter landing site. This scenario would produce the greatest reduction in browse availability for local moose populations. Alternatively, maintaining a diversity of stand age and treatment classes will tend to stabilize browse availability over time in an area. If browse availability is stable in years 2-7, production after year 2 posttreatment would not offset reductions that occur during the first 2 years posttreatment (unlike increases in browse production after timber harvest). Clearcuts at >10 years posttreatment may produce more available browse than untreated clearcuts as suggested by Newton et al. (1989), but the absolute biomass difference will likely be small. Managing the number and location of pretreatment and posttreatment clearcuts is a more certain approach for maintaining browse availability. Staggering treatment times of neighboring clearcuts by >3 years will help reduce fluctuations in overall browse availability. Greater compensation for treatmerit effects may be needed when pin cherry and aspen dominate clearcuts because browse reductions due to treatment may be greater. If staggering treatment dates of similar-aged clearcuts are not feasible because of reduced silvicultural effectiveness, then management of timber harvest schedules may be required to achieve this objective.

There may be options for increasing the value of treated clearcuts as foraging habitat for moose, but these methods need direct study. There is evidence that moose browse more in sections of clearcuts unintentionally missed by aerial spraying than in treated sections (Santillo 1994). Santillo (1994) estimated that unsprayed areas accounted for 1-10% of treated clearcuts in his study and suggested that intentionally leaving narrow strips of untreated browse may be beneficial to moose and may not substantially decrease conifer regeneration. Leaving areas of untreated vegetation near clearcut edges, where browse is more accessible to moose during periods with deep snow (Thompson and Vukelich 1981) also may increase the value of untreated strips. A 10% increase in browse availability on a 40-ha clearcut will not increase forage-based-carrying-capacity greatly (<0.5 moose) for winter, but small increases in browse availability may allow short-term use of sites as activity centers in the home ranges of moose. More information is needed on conifer regeneration and moose foraging behavior in untreated strips to understand trade-offs between conifer release and browse production. As with moose, the consequences of forest management with herbicides on other taxa will depend largely on habitat requirements of individual species (Lautenschlager 1993) and will change during stand regeneration.

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