EFFECTS OF MOOSE POPULATION DENSITY ON DEVELOPMENT OF FOREST STANDS IN CENTRAL EUROPEAN RUSSIA

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ABSTRACT: When moose population density is high (3–5 individuals per 1,000 hectares), deciduous trees, in particular aspen, are depressed, and cutovers are rapidly overgrown with spruce. Higher moose densities can result in the depression of spruce and degradation of the tree stands. In the near future, preservation of a high population of moose may cause the aspen to disappear and prevent regeneration of pine, oak, and mountain ash. When moose density is 2–3 individuals per 1,000 hectares, the development of stands follows its usual pattern. The composition and structure of modern forests is a function of the pattern of tree stand development on cutovers. According to modern theory, following the removal of coniferous trees on cutovers, deciduous stands are formed, and regeneration of the main coniferous forests is extended over a period of more than 100 years. As a result, coniferous forests are ubiquitously replaced by deciduous.

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During recent years, due to increasing moose populations and associated activities, the natural pattern of cutover overgrowth is substantially modified. A large number of studies of the effect of moose on the formation of stands indicate that selective removal and damage of young forests and species composition of stands have been changed (Dinesman 1961, Elsky et al. 1975, Dunin 1979, Tikhonov 1980, Smirnov 1987).

The present study is an attempt to estimate the consequence of different moose population densities on forests. The fate of different tree species and the pattern of stand development were inferred from comparing stands on cutovers of different ages, for which a set of different-age cutovers were selected. The research was performed in the Kostroma, Moscow, and Yaroslavl Regions, characterized by different moose population densities: 2–3 individuals per 1,000 ha (the Kostroma Region), 4–5 individuals per 1,000 ha (the Moscow Region), and 6–10 individuals per 1,000 ha (the Yaroslavl Region).

The most important forage habitats of moose are at present associated with increasingly overgrown cutovers, where young stands of early successional trees provide the necessary food for the animals. The cutovers are primarily overgrown with birch (*Betula* spp.) and aspen (*Populus tremula*) that, in the absence of moose, after 5–10 years form a deciduous canopy, which for a long time depresses regrowth of primary coniferous species. This pattern of overgrowth of cutovers in the regions under consideration was observed in the 1950s and 1960s, when the moose population density was low.

RESULTS AND DISCUSSION

Currently the overgrowth of cutovers, under increasing activities of moose, proceeds differently in various regions. In the

Moscow Region, the cutovers are actively overgrown with deciduous trees, the aspen predominating. Of all the cutovers under study, the aspen was superior or slightly inferior in the number of stems compared to other trees. During the first years, aspen root shoots substantially exceeded other species in growth. At a 2-year-old cutover, the average height of aspen reached 1.6 m, while in other species it did not exceed 70 cm, and birch, which ranked second in abundance, was equal to only 25 cm (Table 1). Some individual groups of aspens formed shoots, or under weak activity of moose at this cutover, an aspen canopy would develop in several years.

However, as early as the first year, the aspen was under heavy browsing pressure by moose. Almost all the aspen forests were browsed by moose at a height of about 1 m (Table 1). Characteristically, browsing did not affect the state of aspen, and new regrowth averaged 60 cm in length. Overall, 93% of the aspens were browsed, while other species were virtually intact (except the mountain ash).

A similar pattern was observed in other overgrowing cutovers. At a 4-year-old cutover, where there were fewer aspens, most of the trees were removed annually by the moose. Hence, despite the age of 4 years, the height of aspens was only 87 cm. Nevertheless, their condition was still good, and the annual regrowth of the top shoot reached 61 cm (Table 1).

During subsequent years, an active selective removal of the aspen continued. In all the cutovers, the aspen stems were removed by moose at a constant height, and the aspen formed regrowth of about 1 m in height, irrespective of age. At a 17-year-old cutover, as a result of annual removal, all the aspens were depressed and weakened, 90% of the stems were dry, and the entire aspen forest was a growth of semi-dry stems. Despite the great age of this aspen (7–14 years), its average height was 93 cm, and the average size of annual increment was only 33 cm, the stem diameter being 12 mm (Table 1). Thus, despite its great resistance to removal, the aspen was weakened and dried in all of the sites, yet continued to be among the regenerating species of the cutover.

In addition to the aspen, less abundant trees, such as oak (*Quercus* spp.), mountain ash (*Sorbus aucuparia*), and maple (*Acer* spp.), were also controlled by moose. Due to active browsing of these trees by moose, these trees remained in the zone of influence and were not involved in the formation of the stand.

The overgrowth of the cutover by other species followed a different pattern. Birch, substantially inferior to aspen during the first years, subsequently became dominant. At a 17-year-old cutover, the birch was substantially superior to aspen in height, and became a dominant species (Table 1). Quite a number of species were not included in the zone of moose influence. Nevertheless, 80% of the birch proved injured, and the average height of these trees was only 144 cm (Table 1). Hence, the birch formed only rare stands.

Of special interest in these conditions was the regeneration of spruce (*Picea* spp.), which occurs in the clearings mainly in the form of forest plantations and which is the primary species of these forests. At the clearings examined, spruce regrowth was virtually undamaged by moose. The spruce surpassed the height of the deciduous trees, getting out from under the canopy of the stand. At a 17-year-old cutover, it considerably outstripped other early successional species in growth and reached the developing stand.

In the Yaroslavl Region, where the population density of moose is higher, moose still substantially affect the development of stands. During the 1950s, when the moose

Table 1. The state of regrowth at cutovers of different age in the Moscow region.

Species	Age (Years)	# stems per ha	Stems Browsed by Moose		Height (cm)	Length of Annual Shoot (cm)	Stem Diameter (mm)
			#	%			
			2- year-old cutover (1987)				
Aspen	2	71,320±18,060	66,220±1,624	93	159±2.4	62	10.7±0.27
Birch	-	38,000±4,218	0	0	25±1.8	-	2.1±0.21
Linden	-	13,320±2,230	0	0	71±2.8	-	7.3±0.50
Willow	-	-	0	0	1±5.2	-	-
Mountain Ash	-	-	-	56	69±5.4	-	-
Spruce	-	2,660±330	0	0	30±3.0	-	2.6±0.24
			4-year-old cutover (1985)				
Aspen	4	10,000±2,940	7,840±2,894	78	87±2.6	61±3.1	8.8±0.39
Birch	1-4	16,934±4,218	1,280±616	8	80±3.5	-	6.2±0.31
Willow	1-4	7,866±2,230	2,140±1,116	27	79±4.2	-	6.4±0.47
Mountain Ash	1-4	rare		40	75±3.3	-	5.8±1.16
Spruce	-	934±330	0	0	67±8.8	-	12.4±2.55
			17-year-old cutovers (1972)				
Aspen	7-14	16,440±3,284	15,880±3,180	97	93±1.9	33±1.5	11.9±0.33
Birch	15-17	7,340±2,120	5,880±1,404	80	144±8.9	-	15.3±1.08
Willow	-	444±346	333	75	83±9.7	-	7.5±1.89
Mountain Ash	-	single	-	100	60±10.0	-	9.5±1.50
Spruce	-	3,334±840	rare	-	150±11.5	-	23.7±1.95

population was low, the cutovers were being actively overgrown with birch and aspen. The spruce remained in the second layer. But, as early as the 1960s, when the moose population density reached 5–6 individuals per 1,000 ha, the aspen was damaged by moose, and lagged behind in growth. At a 19-year-old cutover, the aspen did not exceed 2 m in height, and was behind the growth of other species. In the 1970s, the population density of moose was even higher (up to 10 individuals per 1,000 ha), and the aspen began to be fully removed from the developing stand. At a 7-year-old cutover, there were only dead aspen stands. The birch was also badly injured there. The percentage of injured stems was 80%; hence, birch does not develop a closed canopy, and at the cutover site there were a large number of clearings overgrown with grass.

In these conditions, the regrowth of spruce was also impaired, but it was browsed only rarely and spruce development was not depressed. As a result of the absence of important competition on the part of deciduous trees, the spruce grew very well. At a 7-year-old cutover, its average height was 1 m, at a 19-year-old cutover, 5 m, and by 15–20 years of age, it escaped from the zone of moose influence.

Under these conditions, the spruce, because of moose activities, rapidly occupied the dominant position in the stand, but it should be remembered that with growth of the spruce and with increase in the diameter of the stem, spruce bark may be extensively damaged by moose. Injured in this way, the trees are infected by stem rot and are thus removed from the stand (Smirnov 1987). In the final analysis, the activities of moose at such population density may cause degradation of the developing stand.

In Kostroma Region, where the population of moose is low, they do not notably affect developing stands. During the first years, the cutovers are overgrown with deciduous trees, the birch, willow, and aspen predominating. Aspen contributed to the primary stand only little, and because of this, only single aspen trees were observed at the cutovers. There was no effect of moose on the early successional species, which explains their rapid growth and abundance. At the 3-year-old cutover, their height already reached 130 cm, and at 7–8-year-old cutovers, their height ranged between 1.5 to 2.0 m. Good growth of mountain ash, which is depressed in other regions with high moose population density, is noteworthy. In this case, the number of individuals at cutovers of different age remains consistently high (2.5–3.5 thousand individuals). In the final analysis, by as early as 7–8 years, a dense deciduous canopy is formed.

In such conditions, spruce is sharply lagging behind the deciduous trees. By the age of 7–8 years, it reaches the height of only 70–80 cm (as opposed to 200 cm in the birch), remaining under the canopy of deciduous trees. Thus, the Kostroma Region, with a low density moose population, exhibits a common pattern of overgrowth of cutovers, leading to replacement of primary coniferous species by deciduous remains.

CONCLUSIONS

The above gives grounds to conclude that in regions with increased density of moose populations, the moose has drastically changed the pattern of development of stands in clearings, which was manifested in the depression of growth of deciduous, in particular, the forage species, i.e., the aspen, and to a lesser extent the birch. As a result of that, the aspen is entirely eliminated from the developing stand. It can be expected that with preservation of the present-day population of moose, in another 30–40 years, the aspen may completely disappear from these forests as a forest-forming species. The same applies to some

other species, most vulnerable to the effects of moose. This holds for the pine, which has long ceased being a regenerative species. The oak, increasingly damaged by moose, no longer regenerates. The mountain ash, that has until recently been widely distributed and yielding fruit in the forests, at present in regions with high moose density, is represented by injured and depressed individuals, and it practically yields no fruit. Being the least damaged species, the birch predominated at cutovers, but it cannot form a closed canopy there either. The spruce, the primary species of these forests, is the least affected. Liberated by the moose from the depressive effect of the deciduous trees, it grows fast, outstripping other species in relation to growth and reaches the first layer. In this case, the moose causes the regeneration of primary spruce stands to accelerate. Since some of the birches are preserved, being involved in the formation of the stand, there are grounds to believe that at the site of cutovers, mixed spruce-birch stands will be formed. Characteristically, all these features were previously noted for other regions; in particular, for the forests of Byelorussia, Leningrad Region, and Siberia (Elsky et al. 1975, Dunin 1979, Tikhonov 1980). This suggests the phenomenon observed is quite common.

Where moose density is low (under 2–3 individuals per 1,000 ha) (Kostroma Region), its activity does not noticeably affect the formation of stands. However, where the moose population density is very high (>5 individuals per 1,000 ha), as has been the case in the Yaroslavl Region, moose activity depresses the growth of aspen and also that of spruce and birch, which results in degradation and decomposition of stands. Under such conditions, the result of moose activities cannot in its complexity of effects be easily predicted.

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