The Impact of Herbivorous Mammals on Woody Vegetation at the Different Stages of Forest Succession

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Abstract

The effects of herbivores on the forest woody vegetation were and still are under the spotlight as animals profoundly affect vegetation patterns and processes. Meanwhile, over the last decades, changes in their distribution assumed a very unusual character. The aim was to reveal the changes in animal impact on woody vegetation depending on the forest succession. I used the integrated method of line transects (100 x 4 m) and sample plots (50 x 2 m). The duration of the non-vegetative period determine the time and extent of animal impact to the woody vegetation. The protracted period impelled the distribution of animals in the early successional forests where living conditions meet animal demands. Moose most closely relate to the damaged area (r=0.55). Roe deer and hares are attributable to the early successional seres despite their classical attribution to the species group of the second succession stage. The key indices of climatic factors could be used to predict the impact of herbivores on forest succession.

Key words: herbivores, forest succession, impact, woody vegetation.

Introduction

It is obvious that a forest is not only vegetation while a succession is not only changes in the vegetation, though plant fluctuations cause fluctuations of other biotic components correspondingly. Therefore the changes in the forest producers cause appropriate qualitative and quantitative changes in the species composition, relationship and in all trophic chain of consumers including herbivorous mammals. An increase in the number of pests and damage of the main producers (trees) induces changes in the number of other consumers enhancing the attractiveness of damaged trees for herbivores through the compensatory abilities of plants and allowing overspread of insect pests and fungal diseases (Belova 2010). Therefore, species of herbivorous mammals as an integral part of forest ecosystems are nothing less than passive consumers in the trophic chain. The effects of herbivores on the forest woody vegetation were and still are under the spotlight as animals profoundly affect vegetation patterns and processes. The interdependence between herbivorous mammals and forest succession is well understood. Some studies range over the response of animals of early successional stages to changes in landscapes during the evolution; however, in regard to animals, successions have not been studied more properly (Johnston and Odum 1956, Dasmann 1966, Helle 1985, Ricklefs 1990, Davidson 1993, Lepš et al. 2001). There are some data on the response of animals of the early successional stages to the changes in landscape during the evolutionary process (Ambuel and Temple 1983, Litvaitis 1993, Côtè et al. 2004, Hodson et al. 2011, et al.). There it is in North America, an incongruity between successional stages of animals and plants has been stated expanding agricultural lands and decreasing forest areas (Johnston and Odum 1956, Helle 1985). R.F. Dasmann (1966) has emphasied an importance of determination of wildlife successional groups such as climax, medium or early succesional animals. In the investigations of succession of ecosystems and their components, animal population dynamics are most under spotlight including changes in resources and carrying capacity in their habitats by reason of climate changes (Odum 1986, Ricklefs 1990).

There are many studies on wildlife habitats, attractive forest successional stages and preferable food. Herbivorous wildlife species modify forest succession altering or eliminating forest regeneration. It is evident that animals most relate to the stage where they will obtain an available amount of resources. It could be habitats of the early successional stages while other stages also can be attractive. Nevertheless, most studies have been directed at herbivore damage of forest over time i.e. herbivory influence on successional changes (Horn 1975, Augustine and McNaughton 1998, Hobbs 1996, Reimoser 2000, Yahner 2000, Vavra et al. 2007), particularly on early successional habitats (Lavsund 1987, Gill 1992, Lyly and Saksa 1992, Heikkilä and Härkönen 1993, 1996, Bergquist and Örlander 1998a, b, Bergquist et al. 1999, Yahner 2000, Bergquist, J. et al. 2001, Bergquist, G. et al. 2001, Kullberg and Bergström 2001, Litvaitis 2001, Cassing et al. 2006, Heikkilä and Tuominen 2009). An influence of forest logging of animal foraging and nutritional value of food (Gill et al. 1996, Reimoser and Gossow 1996, Rea and Gillingham 2001, et al.), animal impact caused to forest of the certain age class (Padaiga 1994, 1996, Ammer 1996, et al.) has been investigated.

On the regenerated cutting areas and 14-year-old burning areas, animals find the most available phytomass (Lautenschlager et al. 1997, Hunter et al. 2001, Litvaitis 2001, Trani et al. 2001). Meanwhile resources of preferable plants are fast recovering (Bergstrom and Bergquist 1997, Edenius et al. 2002), there are changes in a microclimate, temperatures, lighting and water regime, the certain part of young plantation is under hauls. All these factors affect the initial plant composition and diversity.

Over the last decades, changes in animal distribution assumed an unusual character. In the different seasons, the certain factors or their permutation have the different limiting importance for the certain animal species incl. the age structure or sex ratio of their population. Increased changeability and the number of extreme events cause changes in the distribution, foraging, population parameters of animals and their impact on the environment. The aim of this study was to reveal the changes in .animal effects on woody vegetation as regards the forest succession and the key indices of climatic factors that could be used to predict the impact of herbivores to forest.

Material and methods

The integrated method of line transects (100 x 4 m) and sample plots (50 x 2 m) has been used determining the main forest characteristics of each route unit. The route was estimated by pacing the line transects. Animal abundance and distribution of the local deer and hare populations (i.e. moose *Alces alces,* red deer *Cervus elaphus,* roe deer C*apreolus capreolus* and brown hare *Lepus europaeus* and mountain hare *L. timidus*), and the age structure and sex ratio of deer populations have been assessed using the pellet group count method during the non-vegetative period. In the rectangular sample plots, woody plants and their shoots within the animal feeding space (from h = 0.1 to 2.2 m) were counted. The consumption of shoots in woody species Csh (%) was calculated as the ratio of damaged to undamaged shoots. The critical level threshold of 40-50% of the shoot consumption has been established for the deciduous species and 20-30% for the coniferous species (Padaiga 1996, Belova 2008, 2010). The data were processed using *MS Excel* and *STATISTICA8*. The study area covers pure pine forests in the two different natural regions of the country. Forests were distinguished on the ground of territory delineation for game. All study area was specified by abiotic and biotic factors determining the main key factors for each area depending on the predominant stands and climatic sub-region (after K. Kaušyla - Bukantis 1994, Belova 1996, 1999) and their favourability for animals. The meteorological and forest inventory data have been collected from the local stations and Forest Service considering the delineation of all territory of Lithuania for game animals (Belova 1999). The total route is 693.1 km and the total number of sample plots is 4,255.

Study area

In this paper, study areas of the same category of forests but located in the diametrically different regions are presented such as:

- **Continental** zone of pine forests (Southern Lithuania, 3b *Dzūkų* sub-region; *Cladonio-Pinetum*, *Vaccinio vitis-idaea-Pinetum* are predominating; pine no less than 90%)
- **Littoral** zone of pine forests (Western Lithuania, 2a *Kuršių Nerija* sub-region; *Cladonio-Pinetum*, *Vaccinio vitis-idaea-Pinetum* are predominating; pine no less than 90%).

In the continental pine forests, the sun radiation is one of the highest in Lithuania. Sharp fluctuations within the day and seasonal annual temperature as well as the earliest and the latest frosts are noticeable. The average air temperature in January falls to -5.4 °C while the maximum reaches -40.0 °C. In July, the average temperature is +17.7°C and may rise at most to +37.0 °C (it is the highest in Lithuania).

In the littoral zone of pine forests, there is the largest number of sunny days in Lithuania; the west and south winds are prevailing with the average speed of 5.5 m/s over the year and storms on average comprise 20 days annually. The warming effect of the sea for Kuršių Nerija is stronger (up to 3°C) than in the eastern part of Lithuania. Because of the influence of the sea, autumn and winter are warmer than spring - the temperature differs from the eastern regions by 3 -3.5°C. The air is most humid in winter (up to 82%) and less in spring (76%). The precipitation amounts to 643 mm per year. There are on average 170-180 rainy or snowy days per year. 75% of the annual amount of precipitation falls during a warm season. The snow appears at the end of November; constant snow covering is formed at the end of December or at the beginning of January, which is 10 or 15 days later than in other regions of Lithuania.

Results

On both study areas, the non-vegetative periods have fluctuated notably by their duration (from 59 days in 2007/2008 to 151 days in 2005/2006, 2008/2009, 2009/2010 and 2010/2011) like other conditions that effect animal distribution, foraging and, correspondingly, their impact on succession of forest biotic communities. Unlike the unusualness of previous periods of 2006-2008 and 2008/2009 (hereafter 2009), 2009/2010 (hereafter 2010) and 2010/2011 (hereafter 2011) were close to characteristic average parameters of non-vegetative periods and have lasted av. 151 days. The temporarily warm phases (e.g. in November of 2008 the average air temperature has reached +3.2°C and it was +0.3°C in December up to +10°C in the first part of January) have alternated with cold wintry but changeable weather. Such changeability and contrast in weather negatively affects animals and particularly roe deer health due to its sensitivity to cold. Although the snow cover was not critical for animals (near 20 cm on average), its state was unsuitable for roe deer and for animal foraging because of the snow crust. There is a question what succession stages animals prefer in the different regions.

In the continental pure pine forests, animals have distributed unevenly grouping mainly in the sites of the optimal foraging as plantations of the earliest successional seres. Being previously observed mainly in the old-growth stands, the moose had shifted to the forest plantations. Localities of their gathering vary marginally. In the last two winters of 2010 and 2011, females and juveniles occur mainly in the pine plantations of the 1st successional stage while males gathered in the middle-aged stands (Figure 1) (foraging in the patches under natural regeneration, stand stocking 0.5-0.6).

During the warm and changeable periods, hares and roe deer have preferred early successional plantations; nevertheless, animals have also distributed in the middle-aged stands and plantations more in comparison with the severe wintry periods in 2010-2011 when their distribution has assumed the similitude of the clumped distribution (Figures 2, 3). It shows the unfavourable living conditions (Belova 1996, 1997, 1999). In plantations of the early-successional stage, the occurrence of hares fluctuates depending on the successional seres with the maximum in the second sere (Figure 3).

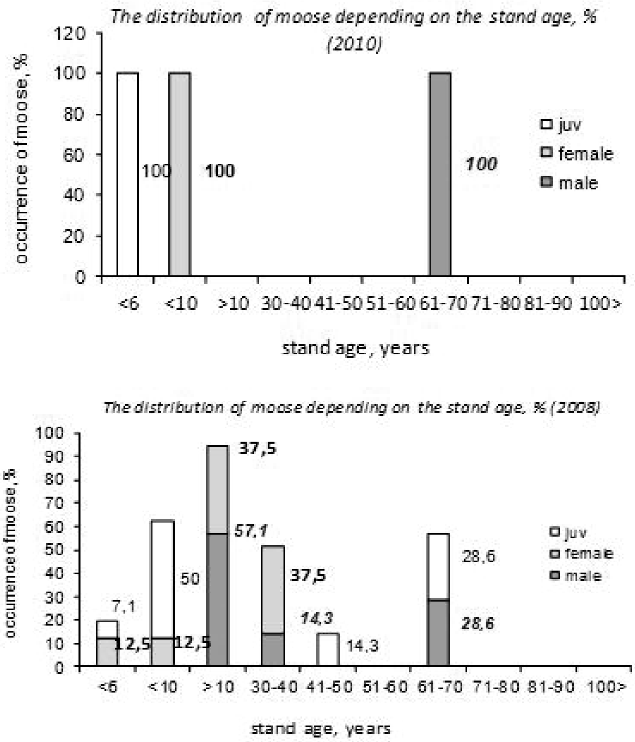

Figure 1. The distribution of moose in the continental pure pine forests depending on the stand age in 2010 in comparison with 2008

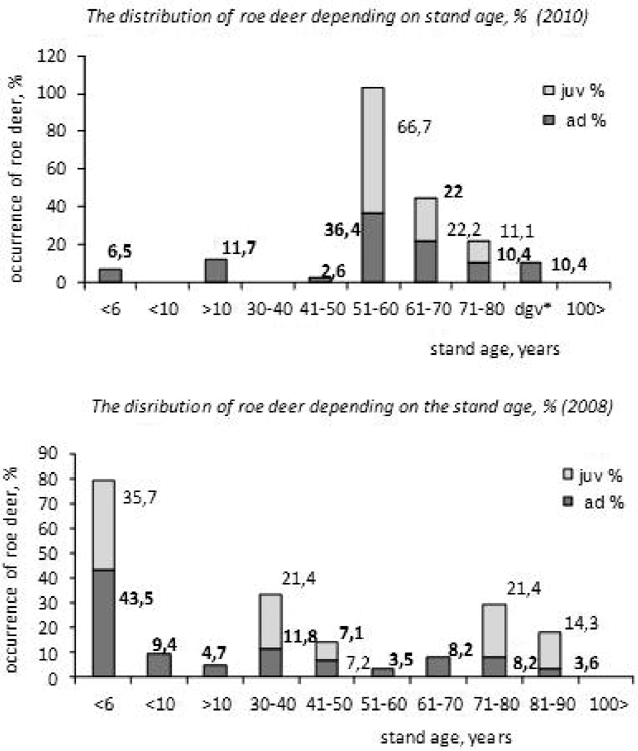

Figure 2. The distribution of roe deer in the continental pure pine forests depending on the stand age in 2010 in comparison with 2008

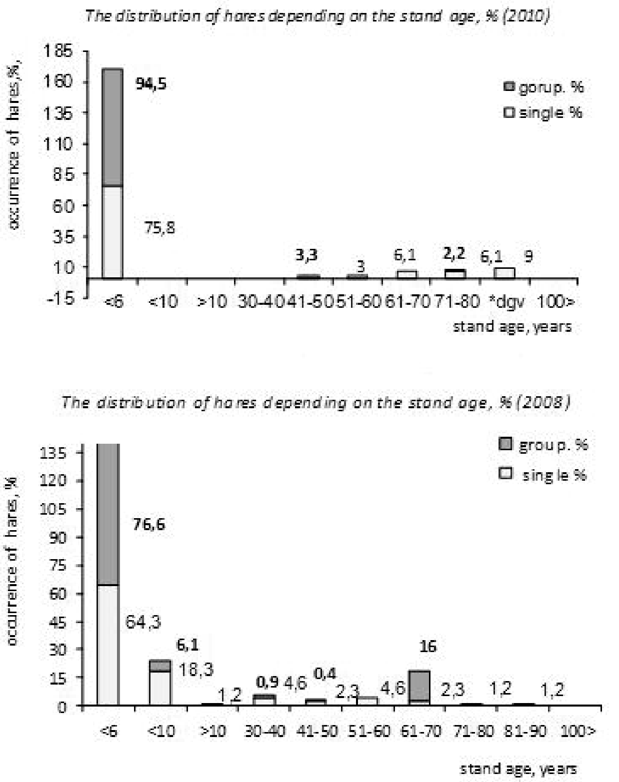

Figure 3. The distribution of hares in the continental pure pine forests depending on the stand age in 2010 in comparison with 2008

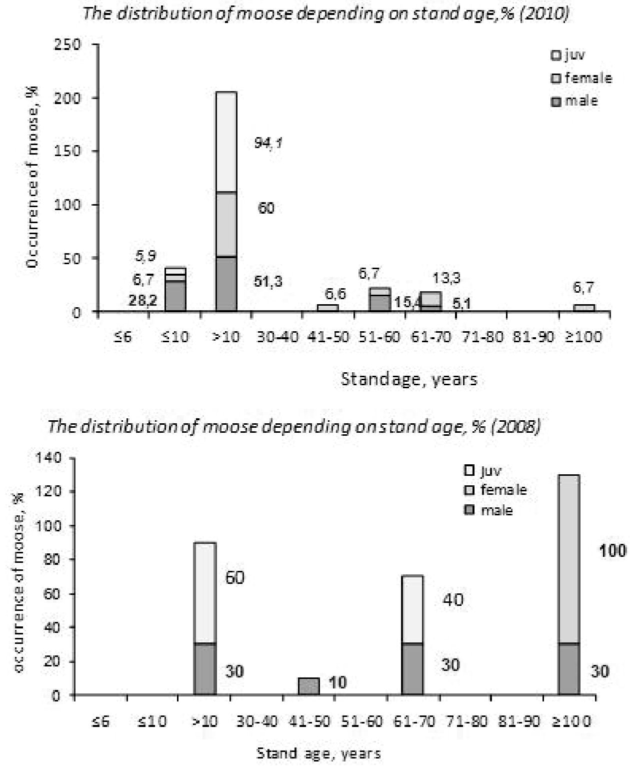

Figure 4. The distribution of moose in the littoral pure pine forests depending on the stand age in 2010 in comparison with 2008

The sparse red deer occur sporadically (there their population density reached only 1 individual per 1,000 hectares) gathering mostly in the scarce sites of middle aged stands *Picetum – Pinetum – Betuletum – myrtillosum.*

In the littoral zone, the snow factor has lost its importance as the limiting factor in the next to last period. In contrast to the warm periods as in 2008, moose have shifted to the young pine stands (10-15-year-old). Roe deer have distributed more evenly than in the continental forests preferring the middle-aged stands and old-growth forests. Hares prefer mainly 10-20-year-old and younger stands in the dunes, foredune ridge and strip of accumulative sand plain (*palvė*) covered by Scots' pine (*Pinus sylvestris*) stands (Figures 4-6).

Unlike moose, the distribution of roe deer and sparse red deer (single individuals) come more even in default of the factors that limit animal moving and foraging in the usual winters (marked fluctuations in the temperatures and snow cover). In such a situation, animal impact is not concentrated in places of the favourable foraging (forest plantations and natural regeneration in dunes) while moose gathering causes stronger impact. Following the increase in number of roe deer and moose, the consumption of pine and

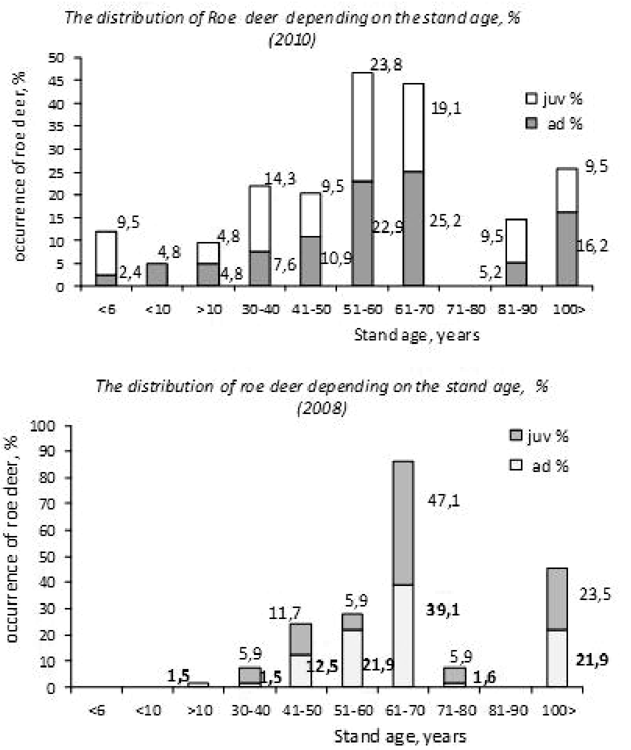

Figure 5. The distribution of roe deer in the littoral pure pine forests depending on the stand age in 2010 in comparison with 2008

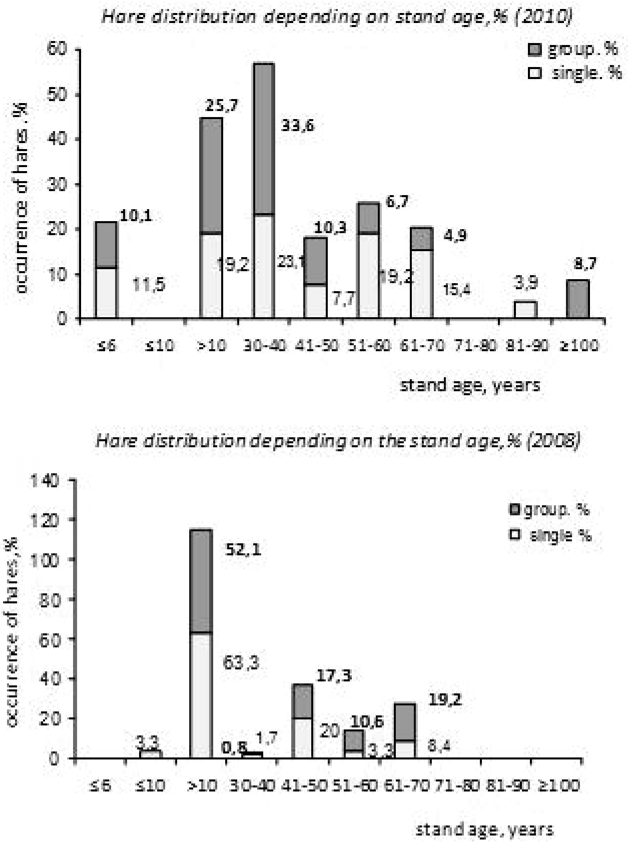

Figure 6. The distribution of hares in the littoral pure pine forests depending on the stand age in 2010 in comparison with 2008

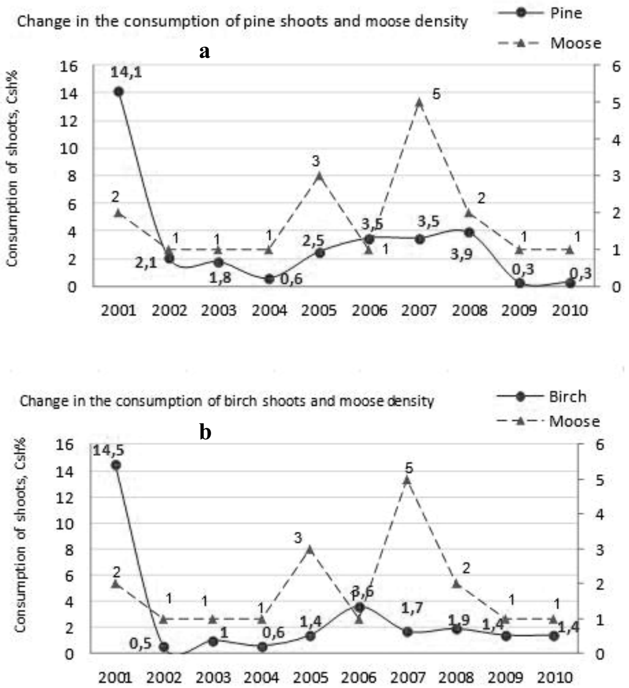

Figure 7. Changes in the consumption of pine (a) and birch (b) shoots and moose density n/1,000 ha in the continental pine forests

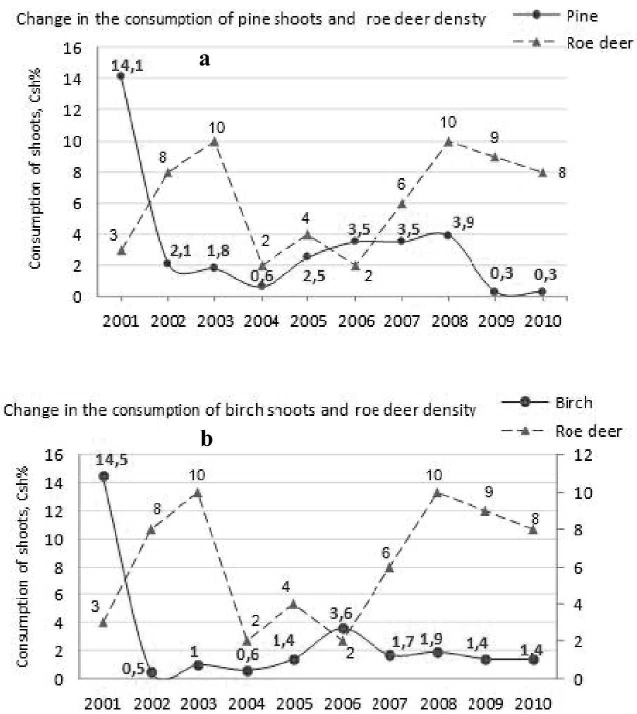

Figure 8. Changes in the consumption of pine (a) and birch (b) shoots and roe deer density n/1,000 ha in the continental pine forests

spruce has changed too. There in the continental pure pine forests, the consumption of all woody species was less than the critical level (e.g. *Pinus sylvestris* L. Csh = 0.4% and *Betula pendula* 0.8%) (Figures 7, 8), excluding willows *Salix* sp. (Csh=73.8%).

In the littoral area, birch consumption was also low (3.9%) and pine consumption did not reach the critical level (11.5%) (Figures 9, 10).

Roe deer and hares most related to *Sorbus aucuparia* damage (r=0.39, p=0.30 and r=0.53, p=0.14, respectively) while moose less damage rowan (r=0.22, p=0.57). Although the consumption of woody vegetation is below the critical level and herbivore populations are not numerous, there is a strong positive correlation between moose density and the consumption of pine shots (r=0.75, p=0.021) (Figure 11). The consumption of pine shoots correlated negatively to the roe deer density. It shows that moose should be considered as a key factor of potential pine damage. The moose damage rate increases rapidly when the population density exceeded 3 individuals /1,000 ha.

The pine is damaged mainly in the patches close to the plantations of pole stage and mature stands. A close relation between the consumption of the pine shoots and deer density was revealed (R= 0.55 ±0.01, *t*=22.56).

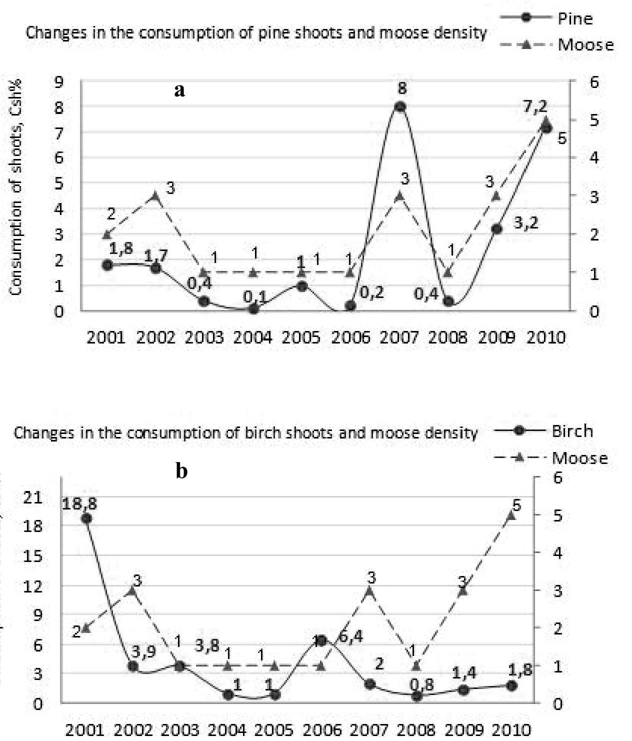

Figure 9. Change in the consumption of pine (a) and birch (b) shoots and moose density n/1,000 ha in the littoral pine forests

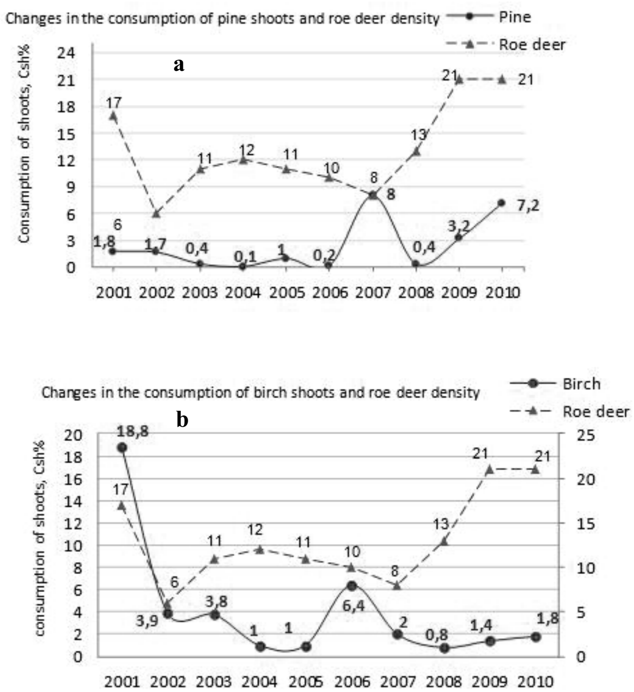

Figure 10. Change in the consumption of pine (a) and birch (b) shoots and roe deer density n/1,000 ha in the littoral pine forests

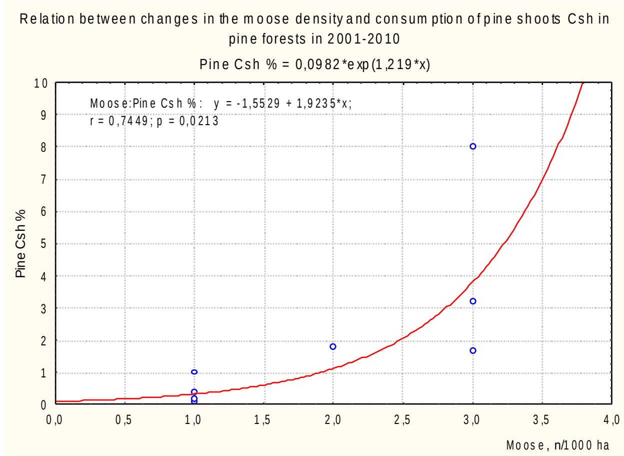

Figure 11. Relation between changes in moose density and consumption of pine shoots Csh% in pine forests in 2001-2010

There is strong positive correlation between herbivore number and damaged area (r=0.66±0.19, R^2=0.42, p = 0.019, F=4.30). The positive relation is revealed between changes in the weather temperatures and damaged area r= 0.57. There is negative close relation between the consumption of shoots Csh% and the average temperatures in the non-vegetative period (r= -0.4). The temperature minimum in the non-vegetative period and damaged area less related r=0.22. The number of different animal species and damage caused by these species to forest relate differently. E.g., roe deer impact on the forest vegetation is more dispersal. Roe deer weakly related to the damaged area (Figure 12) (r=0.21, t=2.82, p=0.01, F=0.9, df =1.2) in comparison with moose (r=0.55±0.19, R^2=0.031, p=0.07, F=8.9) (Figure 13).

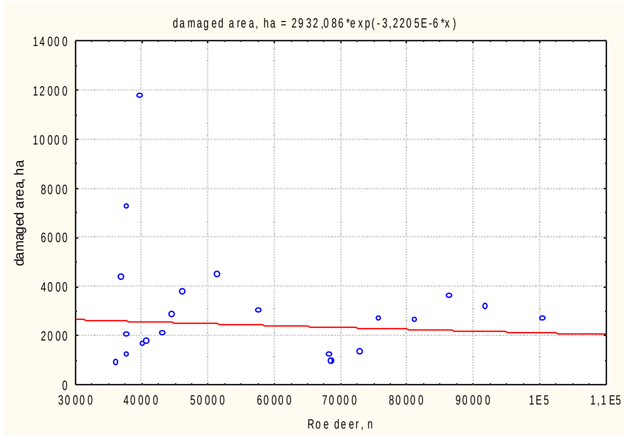

Figure 12. Dependence between an area of the damaged forest woody vegetation and changes in the roe deer number

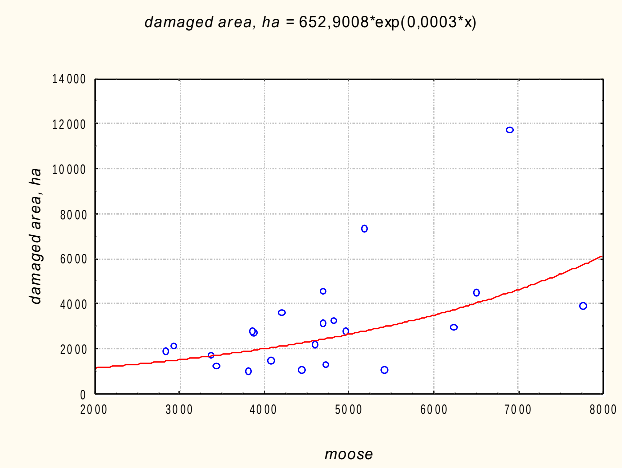

Figure 13. Dependence between an area of the damaged forest woody vegetation and changes in the moose number

The critical level of the snow cover (40 cm by Richter scale for the roe deer) induced animal gathering in the best foraging sites. The thermal changeability acted animal influence on the woody vegetation negatively (R= -0.248±0.022, t= 11.82). The impact of herbivory on the woody vegetation is evident even as they disperse in the sites of the favourable foraging like pine plantations from 6 to 20 –year-old and during the warm periods have selected the old-growth forests.

Discussion

The problem deer-forest is not new and many valuable studies and publications are well known while the item of succession and deer is not properly touched. Many studies have addressed to the certain deer species and particular successional stage (Gill et al. 1996, Jenkins and Starkey 1996, Maier et al. 2005, et al.). This study reveals changes in usual species attribution to a particular faunistic group in the context of forest succession and the role of different species maintaining equilibrium between herbivores and forest woody vegetation.

Depending on habitat preferences, wildlife species have been attributed to certain successional groups (Martynov 1984). The first successional group included only birds and the second group comprises black grouse, mountain hare, roe deer, fox, polecat, least weasel and common vole. Herbivorous mammals should select forest plantations of the second succession stage because of less self-defence of preferable tree species here. It is obvious that succession changes in vegetation effect the self-defence abilities of plants. Early successional plants use less resources for their chemical defence against herbivory in comparison with the late successional stages (Cates and Orian 1975, Ricklefs 1990; Bray et al. 1991, Goralka and Langenheim 1996; Månsson 2004, Gábor et al. 2008). Therefore early successional plants are more important and attractive for animals than plants of late successional stages. Resulting from the animal-plant coevolution, herbivorous mammals have adapted to feed on the certain plant species, selecting namely the annual shoots (Belova 1995, 2003, 2004, 2005). It was not clear what forest succession stage, primary or secondary, animals will select, all the more as there are not many localities of the primary succession such as a natural regeneration on the unbroken soils or some patches in the strict nature reserves. It has been ascertained that some animal species have adapted to tolerate larger amounts of secondary compounds (Kalashnikova 1994, Tixier et al. 1997). There are no data on other deer species while we know that roe deer is closer to moose physiologically and morphologically; however, it does not tolerate larger amount of tannins (Bryant et al. 1998). There is a larger amount of proteins and less tannin in the mature stands in comparison with cutting areas and young plantations, and more nutrients are in the bark of trees in the scarcer stands (Happe et al. 1990). Despite this fact, herbivorous wildlife species mainly relate to young plantations.

Our results have shown that under conditions of climate warming and frequent climate anomalies, moose mostly gathered in the habitats of the favourable microclimate because of animal sensibility to the thermal stress (as -5°C in winter) (Tefler 1984, Renecker and Hudson 1986, Schwab and Pitt 1991, Lundmark 2008, Belova 2008) in thaws. The feeding character (browsing or debarking) depends on the winter conditions (Ratcliffe 1989, Faber and Thorson 1996, Padaiga and Belova 2001, Persson 2003, et al.) as the key factors are the changeability of the air temperatures and state of the snow cover (Belova 2005). Browsing is characteristic over the year, while debarking occurs rarely, from November to April with maximum in the February-March. Selection of the feeding type and habitat depends on the change in the environmental conditions. In the last decade, the snow cover lost its previous significance as the limiting factor particularly during non-vegetative periods that lasted only 54-89 days. However, for moose the heat stress could appear in the all habitats excluding the old-growth and wet forests. It is obvious in the warm periods especially in the littoral pine forests. Thus, the weather conditions induce what succession stage and foraging character animals will choose. For the selection of habitats of the certain successional stage and animal impact on woody vegetation during the changeable and atypical winters, the key-factors are the consumption of shoots of woody plants, considering the thermal changeability and the stability of snow cover.

Conclusions

The changeable and atypical weather conditions can cause respective changes in the usual distribution of herbivorous wildlife species and their impact to forest. An increase in the roe deer number and decrease in the moose number are observed in the warm periods. The increase in number of moose and their gathering in the plantations of the first successional stage are evident during the wintry periods (usual duration av. 151 days).

During the changeable and atypical non-vegetative periods the moose gathered in the old-growth forests in the littoral pure pine forests. The climate warming determines less influence of moose on the main tree species in the forest plantations of the littoral pine forests obviously owing to the sensibility of moose to the thermal factor. The distribution of roe deer assumes a trend of more uniform spatial distribution. The herbivores show ability to adapt to recent climate changes through changes in habitats and the consumption of woody plants.

Under climate warming conditions, there is negative close relation between the consumption of shoots Csh% and the average temperatures in the non-vegetative period. The increase in moose and red deer numbers will negatively affect woody vegetation, and the further warming and climatic anomalies would cause an increase in the damaged area in the continental pine forests. It is necessary to consider the competition between the different herbivore species, which inhabit the same habitats, and the climatic/natural regions.

The duration of the non-vegetative period determine the time and extent of animal impact to the woody vegetation and selection of habitats of the certain successional stage. The protracted period impelled the distribution of animals in the early successional forests where living conditions meet animal demands. Moose most closely relate to the damaged area. Moose damage rate to pine increases rapidly if the moose density exceeds 3 individuals/1,000ha.

However, prohibitions in the regulation of moose population (selective hunting) and an approval of the unsuited terms of hunting season (i.e. disregarding of changes in fluctuations of non-vegetative period and climate anomalies) suppress striving for the optimal structure of local populations.

Although herbivore densities are comparatively low in the pure pine forests, in the continental Southern Lithuania, moose and roe deer most closely and directly related to the pine damage ($r = 0.507$ and 0.506, respectively). In early-successional stage plantations, the moose is potential factor in the pine damage ($r=0.36$, $p = 0.34$). Moose damage rate increased rapidly when the population density exceeded 3 ind./1,000 ha. Changes in early-successional seres determine the animal occurrence and their impact on woody plants depending on the animal species and origin of vegetation (natural or planted). The roe deer was the key-stone species by its impact on the pine already in the initial successional seres. In plantations of the early-successional stage, the occurrence of hares fluctuates depending on the successional seres with the maximum in the second sere. Roe deer and hares are attributable to the early successional seres despite their classical attribution to the species group of the second succession stage.

In the littoral zone of pine forests, the trend of uniform distribution of roe deer is evident. This species mostly occurred in the mature and middle-aged stands with deciduous undergrowth. Moose mostly gather in the mature pine forests in the littoral area, while they only rarely occurred (4.4%) in the young forests and pine plantations. Only during the colder phases animals occur in the older >10-year-old pine forests attending forest gaps and other open places marginally. The changeable winter weather disturbs herbivory in the open places. The animals did not concentrate in the most favourable feeding habitats, and their influence on the woody vegetation decreased.

During all observed non-vegetative periods the repeated browsing is evident especially of the Scots pine (*Pinus sylvestris* L.). The consumption of the unpreferred food as birch (*Betula* spp.) decreased from 18.8% in 2001 to 0.90% in 2007. The decreased consumption of unpreferred food indicates the sufficient availability of the preferred foods while the density of studied animal species was varied marginally.

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ВЛИЯНИЕ РАСТИТЕЛЬНОЯДНЫХ ЗВЕРЕЙ НА ДРЕВЕСНУЮ РАСТИТЕЛЬНОСТЬ РАЗНЫХ СТАДИЙ СУКЦЕССИИ

О. Белова

Резюме

Влияние различных видов растительноядных зверей на древесную растительность лесов была и остается в центре внимания, по причине их значительного воздействия на лесные сообщества и процессы. Но в последние лесятилетия изменения в их распределении приняли значительно необычный характер. Цель работы была определить измнения во влиянии зверей на древесную растительность в завимимости от сукцессии леса. Использован интегрированный метод линейных трансект (100 х 4 м) и учетных площадок (50 х 2 м). Продолжительность невегетационного периода определяет время и степень влияния зверей на древесную растительность. Удлинение невегетационного периода вынуждает зверей локализироваться в молодняках ранних сукцессионных серий, где жизненные условия удовлетворяют потребности зверей. Лоси наиболее связаны с территорией повреждения (r=0.55). Косуля и зайцы относимы к ранне сукцессионным сериям в отличии от их обычной классификации как видов второй сукцессионной стадии. Ключевые индексы климатических факторов применимы для прогноза влияния зверей на сукцессию леса.

Ключевые слова: растительноядные, сукцессия леса, влияние, древесная растительность