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REVIEW PAPER

Wildlife damage to forest stands in the context of climate change – a review of current knowledge in the Czech Republic

Pavel Brabec[1], Jan Cukor[1,2], Zdeněk Vacek[1]*, Stanislav Vacek[1], Vlastimil Skoták[2,3], Richard Ševčík[2], Zdeněk Fuchs[1]

[1]*Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 129, CZ-165 21, Prague 6-Suchdol, Czech Republic*

[2]*Forestry and Game Management Research Institute, v. v. i., Strnady 136, CZ-252 02 Jíloviště, Czech Republic*

[3]*Mendel University in Brno, Faculty of Forestry and Wood Technology, Zemědělská 1, CZ-613 00 Brno, Czech Republic*

Abstract

Wildlife damage to forests has become an increasingly serious problem in recent years, and its impact is exacerbated by ongoing climate change. Rising temperatures, prolonged droughts, uneven precipitation distribution, and other factors affect forest ecosystems, which, in turn, affect cloven-hoofed animal populations, their food preferences, and ultimately, the extent of damage they cause. Based on 133 references, this review article focuses on the relationships between wildlife damage and climate change and presents possible strategies to address this issue in the Czech Republic. Wildlife damage includes not just browsing and fraying in natural and artificial regeneration but also damage to trees from bark stripping and the lesser-known rooting of seedlings. Concerning tree species, browsing is most damaging to silver fir (*Abies alba* Mill.) and sycamore maple (*Acer pseudoplatanus* L.). The enticement to wildlife increases as the proportion of the tree species in the stand decreases. Browse damage is more severe at the edge of the stand. Bark stripping and secondary rot cause the most damage to the production quality of Norway spruce (*Picea abies* [L.] Karst.). Total wildlife damage increases with elevation. Combined with the progress of climate change, game-induced damage significantly restricts close-to-nature forest management practices and limits the use of adaptive measures in response to climate change. In addition, mixed forests with species that attract wildlife and the rapid increase in the number of clearings following bark beetle salvage logging significantly increase game pressure. This is primarily the result of the overpopulation of native and introduced game species and the considerable inconsistency between forest and hunting management practices, with the latter not respecting the principle of ecologically tolerable game damage.

Key words: browsing; bark stripping; fraying; rooting; forest management

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1. Introduction

Climate change, especially increased average temperatures, short-term temperature extremes, changes in precipitation distribution and totals, as well as other adverse climatic events, have a critical impact on the health of forest ecosystems (Seidl et al. 2017; Hartmann et al. 2022; Vacek et al. 2023). In the context of climate change, periods of drought are frequent, particularly in low-lying areas, and the risk of tree infestation by secondary pests and fungal pathogens increases (Sturrock et al. 2011; Lindner et al. 2014). Therefore, it is imperative to adapt forests so that they become more stable not only in terms of health but also long-term sustainability of timber production under the new environmental conditions (Bolte et al. 2009; Lindner et al. 2010; Vacek et al. 2021b, 2023).

The forestry sector faces considerable challenges that derive, on the one hand, from the existing forest structure influenced by previous management practices and, on the other, from the effects of climate extremes (Moomaw et al. 2020). The species composition of newly established stands shifts towards diversity in species and structure, differentiated in height, diameter, and age (Lindner et al. 2014; Vacek et al. 2020b). Mindful of the greater exposure to climatic extremes on open land, even-aged management practices are becoming eliminated in favor

**Corresponding author. Zdeněk Vacek, e-mail: vacekz@fld.czu.cz*

of "uneven-aged," shelterwood, or selection methods. The aim is to allow the growth of stands with high ecological and static stability and, at the same time, substantial economic value (Pretzsch et al. 2017, 2021; Vacek et al. 2021a). For these reasons, the process of replacing declining stands of Norway spruce (*Picea abies* [L.] Karst.) at lower and middle altitudes with mixed stands of suitable deciduous and coniferous species is accelerating in Central Europe. However, in order for these transformation processes to occur, it is necessary to implement a different forest management approach and to significantly reduce game populations, which are often a crucial limiting factor for natural forest regeneration, not only in Central Europe (Beguin et al. 2016; Ramirez et al. 2018).

Large, even devastating damage is generally due to the significant increase in cloven-hoofed populations across Europe that has occurred over the last few decades (Valente et al. 2020; Carpio et al. 2021). Apart from the damage to forest ecosystems, even more serious damage occurs to agricultural crops and damage to solitary trees in agricultural land (Amici et al. 2012; Marada et al. 2019; Mikulka et al. 2020; Månsson et al. 2021). Numerous factors have contributed to this situation and are closely linked to forest management methods. Farmland offers an abundance of energy-rich food for game, and even though this is only a seasonal supply, game can respond quickly by population growth. The mosaics of relatively small forest stands surrounded by agricultural landscapes face escalated pressure in the off season (Massei et al. 2015).

It can be observed that both native and introduced wildlife species are exhibiting an increased abundance (Macháček et al. 2014; Dvořák & Palyzová 2016). Introduced ungulate species thus exacerbate the negative impacts on natural forest regeneration, which was previously influenced only by native species. In Europe, wild ungulate populations grow due to changing agricultural management methods and hunting approaches. Climate change leads to shifts in the animal ranges and often increases the viability of their species (Ruprecht et al. 2020; Bright Ross et al. 2021). In Japan, the population dynamics of sika deer (*Cervus nippon nippon* Temminck) can serve as an example. Between 1873 and 1878, 60,938 to 110,002 sika deer were hunted annually. In 1879, there was a dramatic decline in the sika deer population due to high snow cover and associated winter mortality. The climatic fluctuations pushed the population to the very limit of sustainability, to which the Japanese government responded with a total ban on hunting in the periods 1890–1900 and 1920–1952. In the following decades, periods of prolonged high snow cover have become less frequent, and the sika deer population in Japan is now managed through a landscape pest control approach, with less than half of the population being hunted in a standard hunting mode (Kaji et al. 2010). Due to mild winters and abundant food, sika deer became a successfully introduced game species in Europe, but not without significant negative impacts on native forest ecosystems (Cukor et al. 2019b; Vacek et al. 2020a). Numbers of sika deer continue to rise, as does its range (Biedrzycka et al. 2012), but sika are hunted only as part of standard hunting management. Forced population reduction, preventing the damage to forest stands, has not yet been undertaken.

The distinctive population dynamics encouraged by climate change are also documented for wild boar (*Sus scrofa* L.) (Massei et al. 2015). Climate change increases the frequency of seed years in oak and beech stands, which in turn is reflected in better welfare of the wild boar and higher abundance of piglets, which also reach sexual maturity earlier (Frauendorf et al. 2016). At the same time, wild boars spread to other areas in Northern Europe where unsuitable climatic conditions prevented their presence (Markov et al. 2019). Recently, wild boar and other animals occur all year round at higher altitudes where they were previously absent. The average increase in temperatures also allows wild ungulates that are not in optimal health to survive the off season (Büntgen et al. 2017; Zhou et al. 2022).

This literature review is based on 133 studies and aims to focus on the abundance of game as a principal factor of damage to forest ecosystems in the context of ongoing climate change, and summarize current knowledge on different types of damage such as (i) browsing, (ii) bark stripping, (iii) fraying, and (iv) rooting of seedlings in conditions of Central Europe with a focus on the Czech Republic.

2. Game abundance as a key factor in stand damage

In recent decades, forest ecosystems have been increasingly damaged by both biotic and abiotic factors that significantly threaten their stability (Šimůnek et al. 2020; Vacek et al. 2023). Some of these factors (especially abiotic) can only be influenced to a limited extent. Others, like wildlife, can be mitigated by improved protection of stands or adjustments to hunting management (Vacek et al. 2017). Generally, numbers of the most prevalent cloven-hoofed game species are on the rise across Europe (Valente et al. 2020; Cukor et al. 2022a), in particular, the native European deer (*Cervus elaphus* L.) and introduced species, such as the sika deer and fallow deer (*Dama dama* L.). In some parts of Europe, the abundance of these species already reaches the biological, ecological, or socio-economic criteria defined for game overpopulation (Carpio et al. 2021). In the Czech Republic, an increasing trend is evident for nearly all species of wild ungulates, where the most dynamic development has been documented for the fallow deer over the last five years (Table 1).

The greater the abundance of cloven-hoofed animals, the more pronounced the negative impacts on forest eco-

Table 1. Numbers of hunted game in the Czech Republic between 2018 and 2022.

Game species	Year				
	2018	2019	2020	2021	2022
Sus scrofa L.	137,823	239,818	160,811	230,905	177,877
Cervus elaphus L.	28,287	29,017	29,842	30,792	32,884
Capreolus capreolus L.	102,229	103,018	105,570	107,433	114,100
Cervus nippon nippon Temminck	18,368	17,535	19,382	18,510	19,720
Dama dama L.	23,800	28,978	30,982	33,250	38,653
Ovis musimon Pallas	9,531	10,105	10,580	10,019	10,245

Note: Data are available on the web portal of the Czech Statistical Office (https://www.czso.cz/).

systems and farmland (Heurich et al. 2015; Thulin et al. 2015; Cukor et al. 2017; Marada et al. 2023). Wild ungulate populations in some areas of Europe have reached levels that can be defined as considerably overpopulated (Valente et al. 2020; Carpio et al. 2021). This is not solely attributable to environmental changes, such as alterations in habitat and vegetation conditions. Other factors, including the low numbers of large predators, also play a role (Kuijper et al. 2013; Martin et al. 2020).

The most common types of damage are browsing, winter bark stripping, spring/summer bark stripping, fraying and rooting of seedlings (Gill 1992; Vacek et al. 2014; Skoták et al 2021; Cukor et al. 2022b). However, wildlife influences forest ecosystems also by defecation, urination, carcasses, disturbance of soil surface by rapid increase erosion rate and seed dispersal (Danell et al. 2006; Heinken et al. 2006; Melis et al. 2007; Linnell et al. 2020). Generally, the extent of damage is positively correlated with the population density of the particular damage-inducing game species (Gill 1992). Of the four, browsing and bark stripping are crucial because they lead to the development of secondary damage (Cukor et al. 2019a,b; Vacek et al. 2020a). When the bark is removed, the tree becomes vulnerable to fungal pathogens and the subsequent development of stem rot, and ultimately, the stability of the damaged stand is reduced (Cukor et al. 2020; Hahn et al. 2023). At the same time, the extent of browsing and bark stripping reduces radial increment and production capacity of such damaged trees, particularly Norway spruce (Cukor et al. 2019a,b; Vacek et al. 2020a). Compared to healthy trees, trees damaged by bark stripping suffer primarily from a lack of rainfall in the summer months (Vacek et al. 2020a). Significantly increased game density greatly enhances intraspecific competition and forces herbivores to browse on plants they do not normally seek. Food resources become overexploited, and animals are forced to seek and consume alternatives (Finďo & Petráš 2011). In the case of extremely high game population density, not only palatable but also less attractive tree species are browsed (Borowski et al. 2021). This is common, for example, in the case of a high abundance of fallow deer, which are known to gather in large groups and move and forage in several favored places.

Presently, the interests of forest and hunting management may appear to contradict each other. It must be emphasized that the problem arose either from misunderstanding or narrow, selfish interests. Only a long-term agreement and a joint solution of the stakeholders involved (foresters, hunters, conservationists, and, particularly, landowners) can result in ecologically sustainable game numbers, which is in the interest of both the forest and the game, as well as the whole society (Konôpka et al. 2015; Vacek et al. 2017). However, game numbers should be primarily proportional to the carrying capacity of hunting grounds to prevent game-induced damage. Thus, currently, damage caused by game is a limiting factor for successful forest regeneration, primarily in the conversion of spruce-dominated to species-diverse stands, stable and economically sustainable in the long term (Beguin et al. 2016; Vacek et al. 2019b).

3. Browsing

Browsing is a fundamental aspect that affects the natural regeneration of forest ecosystems (Fig. 1; Ammer 1996; Motta 2003; Bödeker et al. 2021). The process of regeneration is a highly stochastic phenomenon of forest dynamics that depends not only on damage caused by herbivores (and other wildlife species) but also on the habitus of the parent stand, other stand characteristics, including forest structure, story structure, and land use history (Paluch et al. 2019). Spatial and temporal interactions between species are largely dynamic and variable to soil, climate, and stand conditions (Forrester et al. 2017).

Wildlife often damages forest regeneration, hindering regrowth from multiple perspectives (Vacek et al. 2020a). The terminal shoot browsing negatively affects the growth process as such. It slows down the growth of the damaged tree in a given growing season, which is the main negative impact (Schulze et al. 2014). The damaged tree is threatened by reduced vigor and, in the case of repeated browsing, is at mortality risk in subsequent years (Vacek et al. 2014, 2015). However, the secondary effects of damage are crucial, manifested by the suppression of the tree species in natural regeneration. The browsing of woody plants by deer has direct effects on the existence or conservation of plant species in specific habitats and indirectly influences other organisms (Lessard et al. 2012). Cloven-hoofed game – and, especially, browsers – prefer certain species, which results in changes in species composition and consequent uniformity of the surviving stand, depleted of interspersed woody species. Changed species composition is detrimental to less abundant trees that are attractive to wildlife. As a rule, it is silver fir (*Abies alba* Mill.), rowan (*Sorbus aucuparia* L.), sycamore maple (*Acer pseudoplatanus* L.), and other species desirable for forest ecosystems that are browsed (Motta 2003; Konôpka & Pajtík 2015; Vacek et al. 2015). It was confirmed that the foraging attractiveness of tree species often increases with decreasing abundance of a given species in natural regeneration (Ammer 1996; Čermák et al. 2009).

Therefore, browsing can strongly influence not only the species composition, but also the spatial and age structure (Skarpe & Hester 2008; Vacek et al. 2014; Fuchs et al. 2021), which is crucial in terms of forest stand growth under ongoing climate change (Vacek et al. 2023). Preferred tree species are losing competitiveness primarily due to terminal shoot damage (Schulze et al. 2014). The intensity of browsing damage increases with the abundance of cervids in a given location. Damage is not only dependent on the tree species but also on the ungulate species. Thus, cervids may alter interspecific competition between tree species in favor of those they avoid (Vacek 2017; Fuchs et al. 2021). This is true if there is sufficient food supply and extensive natural regeneration. In the case of scarce suitable food and large herbivore populations, less attractive tree species, such as Norway spruce, are also browsed, which results in an overall decimation of newly established stands (Vacek et al. 2022b).

Suppression of species diversity by wildlife or humans leads to the unification of the tree layer (Poleno et al. 2009). Reduced species diversity, in turn, brings about a change in the stability and vitality of the forest ecosystem. Heterogeneous ecosystems have higher productivity at a later stage of development compared to monocultures (Pretzsch et al. 2010; Dănescu et al. 2016; Vacek et al. 2019a; Zeller & Pretzsch 2019). Mixed and richly structured forests are also more resilient to ongoing climate change, manifested by higher mean annual temperatures, uneven distribution of precipitation, and more frequent occurrence of climate extremes. A higher resilience is documented by stable radial increment and increased production capacity of tree species in mixed stands, which is true, for example, for mixtures of European beech (*Fagus sylvatica* L.) and Norway spruce (Pretzsch et al. 2013; Seidl et al. 2017; Vacek et al. 2020b).

Substantial effects of intensive browsing on the structure and dynamics (abundance, height, height growth, and species composition) of natural and artificial regeneration have been described by numerous authors in many locations (Burschel et al. 1990; Modrý et al. 2004; Machar et al. 2018). A more significant damage of artificial regeneration compared to natural regeneration has been confirmed. To some extent, this is because plants from artificial regeneration are usually more developed, show larger annual shoots, and their growth is thus more visually striking, attractive, and nutritious (Čermák 2000; Čermák et al. 2011).

In the Czech Republic, the fifth national inventory of game damage confirmed the considerable influence of game on the health and development of the mixed and deciduous stands, primarily their youngest developmental stages. Compared to the previous survey, the damage caused by wildlife (of any kind) to young stands has increased and exceeds 50% for most tree species. Bud browsing damaged 32% of principal tree species and 57% of the soil-improving ones. Browsing of any kind, i.e. terminal-bud or lateral-branch, was confirmed in 56% of the principal species in the regeneration and 63% of the soil-improving ones (Černý et al. 2016).

An investigation by the Forest Management Institute showed the enormous extent of damage caused by wildlife (Turek et al. 2022). The investigation was accomplished on 1,383 control and comparison plots (CCP) located throughout the Czech Republic. In 70%

Fig. 1. Repeated browsing on the shoot of Norway spruce (left) and European beech (right) in the Sudeten system (photo: Z. Vacek, S. Vacek).

of the tree species, a greater number of individuals were confirmed in the deer fence than in the open, unfenced parts. Browsing or fraying damaged 46% of the willows (*Salix* spp.), 34% of the firs and Douglas firs (*Pseudotsuga* spp.), 29% of the field maples (*Acer campestre* L.), 21% of the elms (*Ulmus* spp.), 19% of the wild cherries (*Prunus avium* L.), and 14% of the ashes (*Fraxinus* spp.) in the regeneration. The average height of saplings of all trees in the fenced part was 90 cm, and in the unfenced part, 65 cm, i.e. in the open areas, the saplings were 28% smaller than in the fences. For 95% of the tree species, the average height in the fenced part of the CCP was higher than in the open area. According to Burschel (1975), Štipl (1999), or Finďo & Petráš (2011), the critical limit for increment size loss is considered to be 25–27%. A greater loss of increment of a specific tree species means the individuals in the stand are damaged so extensively that they start to die. In the surveyed CCP, the critical increment loss threshold was reached or exceeded for 78% of the more frequent tree species. The trees most affected by excessive growth loss are Norway maple (*Acer platanoides* L.) and sycamore maple (*Acer pseudoplatanus* L.) – 58%, wild cherry *Prunus avium* L. – 53%, European hornbeam (*Carpinus betulus* L.) – 52%, poplar (*Populus* spp.) – 51%, rowan (*Sorbus* spp.) – 50%, field maple *Acer campestre* L. – 44%, lime tree (*Tilia* spp.) – 40%, birch (*Betula* spp.) – 39%, oak (*Quercus* spp.) – 34%, ash tree (*Fraxinus* spp.) – 31%, elm *Ulmus* spp. – 25%, fir *Abies* spp., Douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco), European larch (*Larix decidua* Mill.), and European beech *Fagus sylvatica* L. – 25%. Browsing terminal shoots causes a reduction in tree increment in forest regeneration across a vast majority of sites. The disproportionate loss of increment occurred not only locally but in most of the country (Turek et al. 2022).

Further extensive research involving 78 research plots across the Czech Republic shows that sycamore maple and silver fir can be devastated by browsing (77–76% of individuals damaged), while the lowest damage by browsing occurs in European larch (26%) and Norway spruce (28%) (Table 2); Vacek et al. 2022b; unpublished data). According to our review, higher browsing damage has been recorded at the stand edges. However, most pioneer tree species, such as aspen, rowan, and willow (with the exception of birches), are highly attractive for browsing. Therefore, stand management could utilize their potential for the biological protection of commercial species (Myking et al. 2011, 2013; Konôpka et al. 2022).

4. Fraying

In regular game resting haunts and their vicinity, bark damage caused by antlers is typical (Fig. 2; Motta & Nola 1996). Fraying damage is evident on thin stems, where the bark is usually stripped from 30 (40) cm up to 1 m above the ground (Zatloukal 1995). Fraying can cause reduced growth rate and tree deformation. It requires additional management measures, the need for improvement by artificial regeneration, or even loss of the mix, depending on which species of trees the animals choose (Reimoser et al. 1999). Abundant fraying occurs on larches, pines, or Douglas firs (Zatloukal 1995). Territorial marking is analogous to this phenomenon, whereby the bark is torn with antlers on thicker trunks. This damage is typically observed in spruce stands in conjunction with bark stripping, and it is indicative of aggressive behavior, particularly during the rut. Concerning the problem of damage to forest stands, Vodňanský (1997) mentions the danger of incorrect supplemental feeding. Improper methods and timing can result in an increase in browsing and bark-stripping intensity of forest trees.

According to the national forest inventory in the Czech Republic, coniferous trees have a significantly higher damage rate (10.8%) compared to deciduous trees (3.0%) due to winter and spring/summer bark stripping and fraying. Norway spruce is the most affected species,

Table 2. Basic characteristics of areas of interest where permanent research plots are located, and the proportion of browsing damage (%) for selected tree species in the Czech Republic (Vacek et al. 2022b; unpublished data).

Area	Altitude (m a.s.l.)	Plots	AA	FS	PA	SA	AP	BP	LD	QE	FE	CB	PS
Orlické hory Mts.	810–820	4	87.7	59.8	18.4	86.7	—	—	—	—	—	—	—
Krkonoše Mts.	940–1,110	4	100.0	78.4	14.1	76.0	91.1	—	—	—	—	—	—
Broumov area	530–655	6	66.7	51.2	12.0	—	46.8	33.2	7.3	—	—	—	—
Jizerské hory Mts.	640–810	8	68.0	6.0	3.0	82.0	100.0	41.0	—	—	—	—	—
Krušné hory Mts.	635–804	8	—	81.0	31.0	89.0	98.0	83.0	—	50.0	—	—	—
Křivoklát area	444–478	8	—	93.0	—	66.0	97.0	83.0	—	94.0	81.0	97.0	—
Brdy Hills	515–550	8	100.0	91.0	87.0	—	91.0	—	57.0	98.0	89.0	94.0	100.0
Český kras	412–433	3	—	23.1	—	—	64.4	—	—	29.3	40.5	46.7	100.0
Kostelec Pine	410–425	6	—	92.8	19.4	—	—	2.3	—	—	—	—	12.2
Třebechovice area	575–630	6	100.0	100.0	8.0	65.0	—	—	40.0	—	—	—	6.0
Žďárské vrchy	594–620	5	12.0	42.0	15.0	57.0	—	—	—	—	—	43.0	—
Karlovarská Hills	502–652	6	—	8.0	93.0	91.0	92.0	—	0.0	83.0	—	—	—
Tábor area	640–650	6	—	20.0	9.0	33.0	13.0	—	—	13.0	25.0	—	—
Mean			76.3	57.4	28.2	71.7	77.0	48.5	26.1	61.2	58.9	70.2	54.6

Note: AA – *Abies alba* Mill., FS – *Fagus sylvatica* L., SA – *Sorbus aucuparia* L., AP – *Acer pseudoplatanus* L., BP – *Betula pendula* Roth, LD – *Larix decidua* Mill., QE – *Quercus* spp., FE – *Fraxinus excelsior* L., CB – *Carpinus betulus* L., PS – *Pinus sylvestris* L.

Fig. 2. Damage to Douglas fir (left) and Scots pine (right) by fraying (photo: S. Vacek).

with a 13.7% damage rate, which is mainly due to bark stripping. As the altitude increases, the damage rate due to fraying and bark stripping also increases. The most severe damage (17.2%) is found above 700 m a.s.l., while the least damage rate (3.5%) occurs below 400 m a.s.l. (ÚHÚL 2016).

5. Bark stripping

Bark removal by deer from the trunk of coniferous trees in their young to middle age is one of the most pressing problems for silviculture and hunting management (Welch et al. 1988; Gill 1992; Konôpka et al. 2022). As a result, not only is the structure of the wood mass disrupted during the regeneration and wound closure process, but the quality of the wood infected by rot pathogens is also impaired, which is subsequently reflected in economic terms, i.e. by a reduction in the monetization potential of the damaged assortments. Norway spruce is considered to be the most susceptible and most commonly damaged species (Gill et al. 1992; Verheyden et al. 2006; Krisans et al. 2020).

The incidence is determined by various factors, particularly, the abundance of the red deer population and other cloven-hoofed species that cause this type of damage (Cukor et al. 2019b; Vacek et al. 2020a). Other factors include, for example, the species and age composition of forest complexes, their acreage, and, of course, the configuration of the surrounding landscape. The most commonly reported age of damaged stands is 18 to 38 years or 10 to 45 years. The diameter of the damaged trunk is a decisive factor. Earlier studies described that, in young stands, trees with larger diameter at breast height (dbh) tend to be preferred, and as the stand matures, trees with lower dbh are damaged, too (Gill 1992).

However, in the case of bark stripping, secondary effects caused by fungal pathogens have a decisive influence on the further development of the stand, contributing to the decomposition of the wood mass and the gradual deformation of the trunk (Fig. 3; Čermák et al. 2004; Cukor et al. 2019a). The wood of spruce stands damaged in this way can be infested by bleeding conifer crust (*Stereum sanguinolentum* [Alb. & Schwein.] Fr.) during the first year after bark damage. An area of 50 cm^2 of the removed bark can be a sufficient gateway for fungal pathogens (Vasiliauskas & Stenlid 1998). Large wounds in trees at a younger age enhance the probability of rot infections (Vasiliauskas & Stenlid 1998; Lygis et al. 2004) and therefore, damage to very young stands is perceived as particularly disastrous. The range of most suitable temperatures for infection by bleeding conifer crust is between −8.3 and 5.0 °C (Vasiliauskas & Stenlid 1998). This temperature range corresponds to the long-term average in the Czech Republic during the off season, which is 1.7 °C (CHMI 2023). For this reason, winter bark stripping appears to be significantly more problematic compared to spring/summer bark stripping. Stem rot can already extend to 6 m in height or even more in young (ca. 50 years old) intensively damaged spruce stands (Cukor et al. 2019b).

As indicated above, significant impacts on wood quality have been confirmed, especially for Norway spruce, whose value as merchantable timber rapidly decreases due to bark damage and subsequent rot (Cukor et al. 2019a, 2019b; Vacek et al. 2020a). Compared to Norway spruce, Scots pine is significantly less devalued by bark stripping and shows considerable resistance to the spread of stem rot (Metslaid et al. 2013; Cukor et al. 2022b). However, in contrast to the available knowledge on the effects of bark stripping damage to Norway spruce and Scots pine, there is minimal data on the effects and consequences of this damage on silver fir stands. For example, Kohnle & Kandler (2007) report that damage to the bark of silver fir is less severe than that of Norway spruce and point out that fir wood is less susceptible to stem rot. Metzler et al. (2012) cite that Norway spruce, unlike silver fir, has resin canals, which may be the reason for the spread of fungal pathogens after bark injury by game. Injury to silver fir bark by wildlife has been studied in terms of histological changes by Oven & Torelli (1999) and of growth and vigor by Pach et al. (2005, 2008), who point to a decrease in wood quality, reduced vitality, growth of fir trees, and the spread of rot.

This rot typically manifests by discoloration of the wood and faster development up to the complete decomposition of the wood mass. Wood discoloration at the initial stage of decay can be the result of fungal and bacterial presence and the reaction of wood to the negative effects of pathogens (Čermák et al. 2004). Simulated damage to the bark of Norway spruce and silver fir at the tree base by logging and transport machinery and their subsequent healing over a period of two years was investigated by Metzler et al. (2012). Damage to the trunks of silver fir and Norway spruce during logging operations in Germany, with emphasis on bark damage and the occurrence of rot, was addressed by Kohnle & Kandler (2007).

A more detailed description of the bark stripping damage on spruce is given by Vacek et al. (2020a): at the Stříbro location (sika deer), where 77% of spruce trees were damaged, and at the Klášterec nad Ohří location (red deer), where as many as 89% of trees were affected. The mean damage circumference ranged from 28% (Stříbro) to 32% (Klášterec). The rate of stem rot spread was 5.7 cm yr^{-1} in Stříbro and 9.6 cm yr^{-1} in Klášterec. The extent of damage was even more pronounced, with the volume reductions of 50% at the Stříbro location and even 71% at Klášterec (Vacek et al. 2020a). Contrastingly, damage to Scots pine in the Stříbro location was less extensive (Cukor et al. 2022a). Of the number of trees assessed, 62% were healthy (including damage of up to 1/8), and 29% were moderately damaged. Extensive circumferential damage was confirmed in only 9% of pine trees. Again, the spread of rot in pine trunks demonstrated the considerable resistance of this tree species to deer-induced damage. The average rate of vertical spread of rot in the tree trunk was only 0.86 cm yr^{-1}. Pines with low damage rates showed an 11% reduction in volume, while trees with high damage rates showed a 17% reduction in volume compared to undamaged individuals (Cukor et al. 2022a).

Research in the Jeseníky Mountains showed that 81% of fir and 40% of spruce were damaged by bark stripping (Vacek et al. 2022a). On average, the rot reaches from the base of the tree to a height of 1.5 m in fir, while in spruce, 2.5 m. The mean production quality parameters with emphasis on the occurrence of rot after bark stripping damage compared to Norway spruce, silver fir, and Scots pine in the forest district of Janovice (Jeseníky) and of Stříbro (Pilsen) are presented in Table 3. High bark stripping damage together with silver fir also occurs in Douglas fir in condition of Central Europe (Konôpka et al. 2024).

Fig. 3. Cross sections with marked rot – Norway spruce (left) and silver fir (right; photo: S. Vacek).

Table 3. Bark stripping damage and rot incidence in the study plots (Vacek et al. 2020a, 2022a; Cukor et al. 2022a; unpublished data).

Indicator of damage	Jeseníky (red deer)		Pilsen (sika deer)	
	fir	spruce	spruce	pine
Percentage of damaged trees (%)	81.1	40.2	77.3	38.0
Length of damage (cm)	50.1	46.3	39.0	43.3
Initial height of damage (cm)	91.0	105.2	87.9	89.8
Circumferential damage (%)	49.7	23.9	27.8	23.1
First damage (age)	14	13	11	8
The largest extent of the damage (age)	20–28	18–26	16–24	14–22
Mean length of rot (m)	1.5	2.5	1.9	0.7
Maximum length of rot (m)	2.6	5.4	4.5	1.9
Mean volume affected by rot (%)	19.3	33.6	30.1	14.7
Rot spread in the trunk (cm yr^{-1})	6.3	11.3	5.7	0.9

6. Rooting

In the Czech Republic, this type of damage is caused only by wild boar (Fig. 4). It is a systematic destruction of planted seedlings (Fern et al. 2020). In most cases, seedlings are simply uprooted and left on the edge of the hole. Consumption of the above-ground parts of seedlings and roots occurs only to a small extent (Skoták et al. 2021). The reason why boars uproot seedlings has not yet been fully explained. According to one hypothesis, the animals chew the roots to access sap and starches (Wood & Roark 1980) and spit out the remaining part of the damaged seedlings. Another reason may be the aromaticity of some tree species or the way the site is prepared before planting (Mayer et al. 2000). The intensity of seedling damage is likely related to a combination of environmental conditions (food supply, availability and age of seedlings, season, wild boar population density, hunting pressure, soil cover, soil moisture, etc.) (Fern et al. 2020). The rooting of forest tree seedlings occurs in young plantations (Mayer 2009), with the initial four weeks representing a particularly vulnerable period (Skoták et al. 2021). This type of damage has become widespread in recent years. In heavily affected sites, up to 80% (but normally around 5%) of planted trees can be damaged (Skoták et al. 2021). However, the further development of seedling rooting damage is difficult to predict due to multiple factors related to wild boar population dynamics. On the one hand, a population increase of wild boar has been documented in Europe (Massei et al. 2015), and on the other, Europe has been facing the spread of African swine fever in recent years with fatal impacts on local wild boar populations (Cukor et al. 2021).

7. Management of stands endangered by game in the context of climate change

Wild ungulates represent a significant limiting factor to forest growth and, in some cases, to the survival of the forest itself. This is made clear by their impact on forest health, including browsing, bark stripping, and fraying (Tanentzap et al. 2009; Jarnemo et al. 2014; Ramirez et al. 2018). The root cause of the problem, however, is

Fig. 4. An uprooted European beech seedling without (left) and with (right) consumption and spitting out of the roots (photo: V. Skoták).

not the conflict between vegetation and game but rather the divergent interests of human management (Putman et al. 2011). The issue of game-induced damage, which encompasses the imbalanced management of the various components of forest ecosystems and the associated mismatch between forestry and hunting management, has been a long-standing conservation concern (Cukor et al. 2019b).

In preventing damage to forest stands by wildlife, various measures are taken, notably methods of individual or group protection and the use of commercial repellents (Marada et al. 2019; Spake et al. 2019). In young stands, effective individual protection tools for a selected number of target trees include dressing the tree trunk with two or three overhanging branches bent from the top to the bottom (Novák et al. 2023). The branches offer a physical barrier, thereby reducing the access of the game to the trunk (Månsson & Jarnemo 2013). In older stands, bark scraping is recommended, where mechanical disturbance of the bark of coniferous trees (especially for Norway spruce) results in roughening or pitching the tree trunks. Subsequently, the bark on the trunks develops a coarser texture with partial resin cover, rendering them less attractive to deer (Ligot et al. 2023; Novák et al. 2023). Stand management, considering optimal utilization of the forage potential of pioneer species can also significantly reduce bark stripping damage on the stands from the point of view of the high attractiveness of these tree species (Pajtík et al. 2015; Konôpka et al. 2022). Nevertheless, these provisional measures do not address the long-term issue of the continuous increase in population density and the expansion of the distribution range of wild ungulates (Valente et al. 2020; Carpio et al. 2021). The observed changes in ungulate population dynamics are the result of a complex interplay of factors, including the influence of changing climatic conditions (Ruprecht et al. 2020; Peláez et al. 2022).

Climate change in the context of forestry has been addressed by numerous authors (e.g., Spittlehouse & Stewart 2003; Bošeľa et al. 2014; Roshani et al. 2022), where the main topic of study is forest adaptation to global climate change (Brang et al. 2014; Keenan 2015). A myriad of adaptation measures have been devised to address this issue, which take into account the inherent instability of climatic conditions and aim to enhance the flexibility of forest management and reduce the potential risks of damage or destruction of forest stands (European Commission 2014). To maintain the highest possible species diversity in the face of persistent climate change, adaptation measures must be applied at both the temporal and spatial scales (Vacek et al. 2023). In light of these challenges, it is imperative to implement both short-term and long-term adaptation measures. The former considers periodic increases in high temperatures and alternating precipitation deficits, significantly impacting forest ecosystems and their growth (Vacek et al. 2023). Other short-term measures may also include using more resistant provenances of forest tree species and the application of climate variables to forest growth models (Spittlehouse & Stewart 2003). In addition, long-term measures should be discussed, with particular emphasis on the implementation of health selections and other tending interventions. It is also worth noting the use of seed areas and gene bases for the transfer of suitable seeds between other acceptable sites. Additionally, it is necessary to consider modifying the regeneration period of stands and most importantly, minimize damage to stands and the spread of biotic agents, including game (Spittlehouse & Stewart 2003). It is frequently observed that browsing can result in the elimination of certain tree species from their habitats, whether in part or totally (Moser et al. 2006). On some sites, the deer even make it impossible to establish a new silvicultural generation in stands. Significantly increased game densities intensify intraspecific competition, which can force herbivores to browse on woody plants, a behavior that they would not exhibit in the absence of higher food competition (Finďo & Petráš 2011). For these reasons, mixed stands resistant to climate change are often severely damaged by browsing, fraying, and the repeated rooting of seedlings. However, the most detrimental impact of terminal shoot browsing is its inhibition of terminal growth, overall height, vigor, and the tree's capacity to survive the following years (Vacek et al. 2014).

The intensified pressure of the game on forest regeneration has, for the time being, been negated by the implementation of individual forest protection measures, including the protection of artificial plantations by wire fences. The construction of these fences is currently financially supported by the state. However, the measures generally do not protect natural regeneration, essential for growing diverse, climate-resilient forest stands (Vacek et al. 2024). Numerous studies have already shown significantly higher resilience and stability of radial increment in tree species growing in mixtures and coming from natural regeneration compared to trees planted in monocultures through artificial means (Pretzsch et al. 2020; Pardos et al. 2021; Vacek et al. 2021a). In contrast, implementing fencing for game protection can inadvertently elevate the pressure exerted by game on surrounding-open-stands, which may contain natural regeneration. This can result in a further intensification of the negative effects of game pressure. Paradoxically, this often results in the protection of artificial plantings whose resistance to climatic extremes is significantly lower, while natural regeneration is left unprotected. It is evident that the optimal approach to fostering the growth of a robust and adaptable forest ecosystem is to align the objectives of forest management with those of hunting. Rather than investing significant resources in the construction of fencing to safeguard less resilient, artificially planted forests, it would be more prudent to pursue a more holistic approach (Vacek et al. 2024).

8. Conclusion

The damage caused by wildlife must be perceived as a limiting factor for successful forest regeneration, especially when converting spruce-dominated stands into species-diverse, stable, and economically sustainable forests for the long term. However, for forest owners in the Czech Republic, it is often impossible to ensure diverse plantations, as their forests are excessively damaged by game. Furthermore, the current framework of the hunting management system does not allow owners to effectively reduce game numbers on their properties to a tolerable level. However, the Hunting Act requires the hunting ground user to draw up a hunting plan based on, among other things, a comparison of control and comparison areas. Common practice has shown that owners often do not submit analyses of data from control and comparison plots to hunt users for this purpose. This is because enforcement of the adjustment of game numbers is very problematic, even if excessive damage is sufficiently documented. A penalty can only be imposed for non-compliance with the hunting plan on game that is standardized in the hunting area, and only if it is clearly demonstrated that its numbers exceeded the standardized numbers, which is challenging.

The results from the literature review highlight the considerable extent of damage to coniferous forests by cloven-hoofed game in the Czech Republic, and in other countries in Central Europe. In recent years, this damage has been a limiting factor for close-to-nature forest management methods due to the reduction of the resilience of forest ecosystems and the threat to the sustainability of both production and non-production forest functions. Damage by terminal shoot browsing is a significant limiting factor for the vertical growth of self-seeding and promoting regeneration. Wild ungulates have proven to reduce vertical development, resulting in juveniles being maintained for decades in an unproductive state and at a vulnerable height threatened by browsing. The greatest browsing damage reportedly occurs in silver fir and sycamore maple, although increasing the representation of these species in forest ecosystems is highly desirable under conditions of advancing climate change. Bark stripping on coniferous trees and the subsequent invasion of fungal pathogens through the wound reduces both quality and quantity of production and causes significant economic damage. The greatest economic losses due to bark stripping were found in Norway spruce and significantly less in Scots pine and silver fir. The damage to forests, the cost of forest protection, and the loss of production and quality are currently estimated to be in the billions of Czech crowns annually. However, the damage to the ecosystem caused by wildlife is a challenge to quantify. In conclusion, it is crucial to highlight the necessity for constructive communication, cooperation, and harmonization among the interests of hunters, foresters, and farmers moving forward.

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