Lesn. Cas. For. J. 62 (2016) 123–130 DE GRUYTER OPEN DOI: 10.1515/forj-2016-0013

REVIEW PAPER

Lesnícky časopis - Forestry Journal
http://www.nlcsk.sk/fj/

Wind – an important ecological factor and destructive agent in forests

Bohdan Konôpka*[1,2], Peter Zach[3], Ján Kulfan[3]

[1]National Forest Centre, Forest Research Institute Zvolen, T. G. Masaryka 2175/22, SK – 960 92 Zvolen, Slovak Republic
[2]Czech University of Life Science Prague, Faculty of Forestry and Wood Sciences, Kamýcká 129, CZ – 165 21 Praha 6 - Suchdol, Czech Republic
[3]Institute of Forest Ecology, Slovak Academy of Sciences, Ľ. Štúra 2, SK – 960 53 Zvolen, Slovak Republic

Abstract

Wind is both an ecological provider and disturbance facilitator influences trees and other organisms in forests. Impacts of wind on induvidual trees and forests mainly depend on the strength (or intensity) of the wind and the stability of the trees. Wind causes large-scale damage to forests and serious economical losses for the forestry sector within Europe. Therefore, knowledge of interactions between wind and trees and/or forests provides the baseline for developing adequate prevention or mitigation of the negative consequences associated with wind disturbances in forest ecosystems. Herein, we analyse the wind as an ecological and disturbance factor in forests in Europe, emphasising forests in Slovakia. Here, strong winds destroy mostly spruce dominated forests in the following regions; Orava, High and Low Tatra Mountains, Great Fatra Mountains, Pohronie, Poľana Mountains and Slovak Ore Mountains. Increasing volumes of timber damaged by windstorms have been documented since 1961, with the maximum damage recorded in 2004. Yearly volumes of damaged timber of approximately 2.5 mil. m^3 are predicted from 2016 to 2030. This highlights the data requirement regarding wind disturbances for integrated forest protection against dangerous winds and other disturbance agents in forest ecosystems in Slovakia and other European countries.

Key words: wind; forest damage; climate change; Slovakia; Europe

Editor: Jaroslav Holuša

1. Introduction

Wind is one of the most important disturbance dynamics and ecological factors in many types of ecosystems (Ennos 1997). In forest ecosystems, wind influences trees directly e.g. by damaging stems or uprooting, or indirectly e.g. through modifying temperature and soil moisture. Over time, the prevailing wind can shape the morphology of trees. A good example of this are dwarf-like tree forms, flag-like asymmetric tree crowns, converging stems, leaning stems (Fig. 1), asymmetric cross-sectional stem profiles, compressive and tensile wood (Zhu et al. 2004). Influence of wind on forest trees and stands depends on wind strength. Low intensity winds usually do minimal damage to forests, however, strong winds may cause serious damage. As strong winds are infrequent, they only damage forests occasionally. Strong winds destroy interim unstable trees (e.g. trees growing in soils excessively saturated with water) and their stands become unstable in the long-term due to inadequate forest management. Gardiner et al. (2016) classified the types of wind damage to forests from negligible to fatal. He recognized, for example, microscopic damage to foliage, partial or total defoliation, branch breakage, breakage or uprooting at the tree level, gap formation at the community level, and successional changes across space, at a regional level.

Wind influences physiological processes in trees and modifies mechanical and technical properties of wood (Peltola et al. 1999; Gardiner & Quine 2000; Konôpka B. 2000; Zhu et al. 2004). It promotes the dispersal of fungal spores, plant pollen and seeds, and regulates spatial distribution of forest flora and fauna (Grubb 1975; Kozlowski et al. 1991; Belanger & Arbas 1998; Wyatt 2003; Zhu et al. 2004).

Herein, we focus on wind as an important ecological factor and disturbance agent in forest ecosystems and present some of the negative consequences of wind disturbances in European forests, with emphasis on forests in Slovakia.

2. Wind as an ecological factor and disturbance agent

Wind is essential to deliever precipitation, crucial for all types of forest ecosystems (Coutts & Grace 1995). Wind affects evaporation, transpiration, spatial distribution of snow, and regulates temperature and moisture regime in forests (Zhu et al. 2004; Konôpka B. & Konôpka J. 2009). In arid regions with aeolian sand soils, wind causes intensive erosion (Coutts & Grace 1995; Zhu et al. 2004) and may substantially modify the relief (Krippel 1965). Wind contributes to the transportation of industrial pollutants, some of which can affect tree health (Jaffe et al. 1995; Vančura et al. 2000). Wind often transfers sharp particles of various origin and chemical composition. These may cause the abrasion of bark and damage foliage and reproductive organs (Zhu et al. 2002b). Wind also moves particles (e.g. crystals of salt from the sea) causing the intoxication of foliage (Fig. 2). Wind is

*Corresponding author. Bohdan Konôpka, e-mail: bkonopka@nlcsk.org, phone: +421 5314 323

Fig. 1. Leaning stems of Scots pine trees (*Pinus sylvestris*) in the alley shaped by the wind. Photo: B. Konôpka.

Fig. 2. Browning of pine needles due to intoxication with salt brought by the winds from the Mediterranean Sea. Intoxication decreases with the distance from the sea edge. Photo: B. Konôpka.

often in a synergistic relationship to other factors in forests. It promotes forest fires (Letelier et al. 1988) and creates favourable conditions for dissemination of pathogenic organisms, such as viruses, fungi, phytophagous insects etc. (Barnes et al. 1998).

While a breeze or low wind operate almost always in forests, strong winds are much less frequent, and cause disturbances varying in intensity. Disturbance is defined as an event which changes (impair) structure of populations, communities and ecosystems, influences resources and the availability of substrates for organisms, and modifies physical properties of the environment (White & Pickett 1985). Wind disturbances operate independently from or in combination with other disturbances (Letelier et al. 1988). Wind can temporally cause cascade disturbances (Dale et al. 2001). Temporal and spatial occurrence, frequency and intensity, as well as the extent of natural disturbance depends on local, regional and global processes, especially changes in the atmosphere and in particular, the temperature regimes and rainfall (Baker 1995). Models of global climate change suggest stimulative effects of inherent phenomena of changing climate on destructive processes in ecosystems (He et al. 1999). Various modelled future scenarios predict an increase in frequency and intensity of storms (Schönenberger 2002).

"Catastrophic winds" such as storms, hurricanes, tornadoes or typhoons influence forests all over the world (Zhu et al. 2004). Strong winds break branches, stems or uproot trees and result in lower densities of trees in forests due to increased tree mortality (Dale et al. 2001; Zhu 2004; Konôpka B. & Konôpka J. 2009). Knock out of trees by the wind is associated with structural changes in forest ecosystems (Odum 1983). More heterogeneous (structured) forests provide open patches (gaps) and an environment created to develope future generations of trees (Ennos 1997). Very strong winds are known to modify the structure of both pioneer and climax forests (Valinger et al. 1993; Gardiner 1995; Zhu et al. 2002a).

Changes in forest structure caused by wind can be classified as follows: (i) primary damage, occurring within a few hours or a couple of days after wind disturbance, is direct, people may be injured and properties and infrastructure may be destroyed; (ii) secondary damage, recorded over a couple of weeks, months or years after disturbance, is successive and caused by various harmful agents taking part in the process; (iii) tertiary damage, documented over many years or even decades after disturbance, is mainly seen in socio-economic relationships (e.g. forest utilization by man with regard to the availability of resources, esthetical values of forests, other ecosystem services, market and prices, employment possibilities etc). Changes in forest structure due to wind disturbances reflect varying interactions (often synergistic) between the wind velocity, duration of wind, local relief, site and stand characteristics such as water content in soil, tree species composition, tree height, tree density, tree health (Gardiner et al. 2016).

Probability that the trees and forest stands will be damaged by the wind is determined by three groups of factors: (i) weather conditions, (ii) site conditions, and (iii) properties of forest stands (Cremer et al. 1982; Schindler et al 2012). Influence of the wind on forests is geographically specific and the frequency of disturbance differs between regions (Quine 2003). Wind direction, frequency and intensity are influenced by relief (Hannah et al. 1995), and there are no management techniques to deal with this kind of factors (Matsuzaki 1994). Influence of windstorms on forests can be mitigated in part, e.g. by management practices in the type of silviculture and forest protection (Mitchell 2013; Konôpka B. & Konôpka J. 2009; Zhu et al. 2004).

Since wind disturbances are stochastic events, it is not possible to predict their exact occurrence in time and space (Schelhaas et al. 2003b). Temporal and spatial occurrence of winds and their influence on stability and sustainability of forest ecosystems are continuously detected and analysed by modern methods and data processing, e.g. using automatized field devices for continuous measurement, computer tools of GIS, approaches of mathematical modelling etc. (Schelhaas et al. 2002; Blennow & Sallnäs 2004; Zeng et al. 2010).

3. Wind disturbances in Europe

Wind is one of the most relevant natural disturbance factors in Europe. Between 1950 and 2000, wind contributed to 35% of the overall damage from natural disturbance in

European forests, this was followed by forest fires, snow, phytophagous insects and other factors (Schelhaas et al. 2003a). Negative impacts of disturbances on European forests have been increasing during the last 150 years (Gardiner et al. on: www.efi.int). The same is true for disturbances in spruce forests in the eastern Carpathians since 19th century (Svoboda et al. 2014). The gradually increasing damage to forests within Europe has evoked numerous discussions about the causes (Lässig & Schönenberger 2000). Some link this phenomenon to climate change and its inherent processes (Schönenberger 2002; Blennow & Olofsson 2008), while others carefully judge inaccurateness and incompleteness of records from the past (Gardiner et al. on: www.efi.int). Unsuitable forest management resulting in even-aged monocultures, especially those of Norway spruce (*Picea abies*), is also considered as an important source of damage to forests where stands with high stocking density are more prone to wind damage when reaching critical height (Schelhaas et al. 2003b; Mitchell 2013).

The influence of wind on forests varies in frequency and intensity acorrs Europe. The most destructive cases of forest damage are reported from the temperate and boreal zones, especially spruce dominated forests (Peltola et al. 2000; Schönenberger 2002; Skuhravý 2002). Large-scale wind disturbances seriously affect all of the components of forest ecosystems and often cause serious socio-economical impacts, especially in densely populated regions. Even low intensity wind disturbance can cause serious disturbance in urbanized areas through damage to infrastructure and/or alteration of quality of life. On the other hand, large-scale wind disturbances in remote, non-populated areas and regions, e.g. in Siberia, may not cause any serious problems and, often, they are not documented and may remain undetected (Skuhravý 2002).

Serious wind disturbances associated with bark beetle outbreaks within Europe were summarized by Skuhravý (2002). Over the period 1990 – 2010 European forests were hit by several intensive wind disturbances which markedly modified forests and landscapes and had a negative influenced on socio-economical functions. For example, large-scale wind disturbances in western and central Europe were caused by the orkan Viviene (Vivian) on 28 – 29 February 1990, and orkan Wiebke on 29 February – 1 March 1990 (Skuhravý 2002). At that time, as much as 72.5 million m^3 of timber was damaged in Germany (Schelhaas et al. 2003b). In December of the same year, the storms Lothar and Martin hit France, Switzerland and Germany (Skuhravý 2002), causing serious damage to forests. Extremely strong windstorm Erwing (Gudrun) hit mostly Northern Europe on 8 – 9 January 2005. In Sweden only, it damaged a total of 270 thousand hectares of forests (77.5 million m^3 of timber). In January 2009, the windstorm Kiryll swept over western and central Europe and also caused serious damage to forests in Germany, the Netherlands, France and Britain. An extremely strong windstorm Klaus hit on 24 January 2009, damaging approximately 684 thousand hectares of forest (e.g. 45 million m^3 of timber) (Gardiner et al. on: www.efi.int). The majority of excessive wind disturbances within Europe were recorded during the winter when large-scale disturbances are often accompanied or followed by numerous smaller ones.

Attempts to create a comprehensive data set about natural disturbances in forests in Europe were reflected in the activities of the European Forest Institute, with the aim to summarize abiotic, biotic and anthropogenic disturbances in specific countries in the Database of Forest Disturbances in Europe (Schelhaas et al. 2003b). This database contains, for example, information about damage to forests around Nürmberg, Germany, by non-specified leaf-eating caterpillars in 1449 and 1450. The first record of a windstorm included in this database is from Buisson de Bleu in Normandy, France, where a total of 66 thousand trees were damaged on 15 March 1519. Quantity and quality of historical records about natural disturbances in forests varies amongst countries and regions. For example, rich datasets about forest fires are available from Spain and numerous historically valuable datasets about forest disturbances are available in Germany. A list of the most severe wind disturbances during the last few centuries (up to 2015) is available from Wikipedia (link: en.wikipedia.org/wiki/List of European windstorms).

In Slovakia data on forest damage by regional and disturbance regime is regularly collected, processed and archived by the Forest Protection Service in Banská Štiavnica within the National Forest Centre, Forest Research Institute in Zvolen. Data exists since the end of World War II, more detailed information (broken by damage with regard to harmfull agents) is available for the last 55 years.

When observing forest ecosystems worldwide, damage caused by wind disturbance is not as significant as other disturbance mechanisms. For example, a severe decline in *Pinus contorta* has been monitored long-term in the forests of western Canada e.g. in the proviences of British Columbia and Alberta. The decline is mainly caused by synergistic effects of a large sacle outbreak in the bark beetle *Dendroctonus ponderosae* (Scolytinae), milder winters attributed to long-term changing climate and forestry practices such as the suppression of forest fires resulting in large areas of even-aged monocultures of pine. Between 1995 and 2008 severe and widespread damage to pine forests was documented over 14 million hectares (Westfall 2007; Raffa et al. 2008; Robertson et al. 2009; Kärvemo 2010). This area is approximately 7-times larger than the total forest area in Slovakia. Nevertheless, declining mature stands of *P. contorta* are being replaced by young forests composed of pioneer tree species, including pine (R. Alfaro, personal comm.). However, damage to forests cannot be judged by magnitude only. For small countries such as Slovakia, disturbances on a smaller scale may be crucial for the locals and the community.

4. Wind disturbances in Slovak forests

Wind is amongst the most important abiotic factors and harmful disturbance agents in forests in Slovakia (Konôpka J. et al. 2008). Over the last 55 years, there has been an increasing trend in damage caused by wind disturbance in Slovak forests. This is well documented in Konôpka B. & Konôpka J. (2009) where the mean annual volume of timber damaged by wind between 1999 and 2008 was 3.3-fold that of timber damage between 1969 and 1978. The volumes of fallen timber increased after a severe wind disturbance on

19 November 2004 (Kunca et al. 2015). This disturbance markedly modified forests, especially in the High Tatra and Low Tatra Mountains (Kunca & Zúbrik 2006), whereas the impact was less pronounced in nearby mountain regions. In the High Tatra Mountains, this unexpected storm damaged mostly spruce-dominated stands across approximately 12.5 thousand hectares. The estimated volume of damaged timber was as high as 2.5 million m^3 (Koreň 2005), nearly half of the 5.2 million m^3 total volume of damaged timber in Slovakia in 2005 (Konôpka B. & Konôpka J. 2009). Large spruce stands adjacent to the disturbed area were consequently destroyed by bark beetles, the most important of which was the Spruce bark beetle *(Ips typographus)* (Nikolov et al. 2010). The outbreak of *I. typographus* in the Tatra Mountains, persisted until the end of 2014, shifting in space and over time (Zach et al. 2015). After the wind disturbance in November 2004 the amounts of timber damaged by subsequent bark beetle disturbance exceeded the timber damaged by the initial windstorm (Konôpka et al. 2011). This occurred mainly in regions where timber remained unmanaged and unprocessed i.e. without salvage logging (Nikolov et al. 2014).

Damage by strong wind in Slovakia prevailingly occur in spruce dominated forests. For instance, between 1998 and 2007 as much as 2/3 of total damaged timber was damage to spruce trees (Konôpka B. & Konôpka J. 2009). Excessive damage to spruce stands relates to their unfavourable stability due to shallow roots and dense exposed crowns that intercept the wind (Stolina et al. 1985). However, the stability of spruce stands also changes with altitude. Spruce stands in Slovakia are relatively stabile in high altitudes, especially within the spruce vegetation tier above 1250 m a.s.l (Konôpka B. & Konôpka J. 2003). Generally, the number of trees per square unit decreases with altitude. Spruce trees in high altitudes are usually of uneven ages and heights, the canopy is more open, stems are more convergent, crowns are longer, buttresses and roots are larger and trees are well anchored in the soil (Konôpka J. 1977). This enhances the stability of spruce stands related to the performance of the wind (Stolina et al. 1985), even though the wind velocity increases with altitude (Coutts & Grace 1995).

The probability of wind damage in spruce forests, especially in even-aged stands, increases rapidly after a sudden decrease in tree density due to managed thinning or other events that cause selective tree mortality, or due to the creation of new forest edges. Even small alteration of structure (compactness) of a spruce stand may increase the risk of damage from the wind (Mitchell 2013; Zeng et al. 2010). Other factors influencing the stability of spruce stands include e.g. forest fragmentation which exposes individual trees to the wind and bark beetles (Wermelinger 2004; Zach et al. 2009, 2010, 2016) and increased mortality of trees in forests due to intensified disturbance from harmful agents (e.g. bark beetles) related to climate change (Konôpka B. 2007).

Considering the risk of forest destruction by wind in Slovakia, dangerous winds are those of the seventh degree (Stolina et al. 1985) or eighth degree (Konôpka B. & Konôpka J. 2009) of the Beaufort wind force scale. Specifically, the seventh degree represents "moderate gale" with wind speeds of 13.9 – 17.1 m s^{-1} (50 – 61 km h^{-1}) at which trees in a forest are intensively swaying and walking against the wind becomes difficult. The eight degree is a "gale" with wind speeds of 17.2 – 20.7 m s^{-1} (62 – 74 km h^{-1}) that usually breaks branches off trees and walking against the wind is nearly impossible. Based on the analyses of spatial occurrence of winds across Slovakia (Slovak Hydrometeorological Institute, 1971 – 2010) the frequency of dangerous winds is highest in the Low Tatra and the High Tatra Mountains. Both regions experience frequent windstorms but damage in forests here is usually scattered and occurs in relatively small patches (Konôpka B. & Konôpka J. 2009).

According to Koreň (2005) the windstorm that destroyed the spruce forests in the High Tatra Mountains on 19 November 2004 consisted of two main currents: (1) diffusive westerly wind and (2) northerly wind (bora) from over the mountain ridges to the valleys. Although the wind damaged forest stands in high altitudes, especially in valleys, most of the damage occurred in the foothills and in flat open areas of the Podtatranská kotlina Basin (Fig. 3). The highest numbers of damaged spruce trees (mostly uprooted) were recorded in the wetlands and, specifically, in the Kežmarské Žľaby area. The spruce trees that were damaged had weak root anchorage as their root systems were shallow and saturated with water reducing the cohesion between the roots and soil (Konôpka B. et al. 2010b). The wind disturbance in Novem-

Fig. 3. Large-scale wind disturbance in a mature Norway spruce stand (Podtatranská kotlina Basin, 19 November 2004). Photo B. Konôpka.

Fig. 4. Windstorm on 15 May 2014 damaged also man-made stands of Scots pine (*Pinus sylvestris*) and European larch (*Larix decidua*). Broken and uprooted 8 years old pine trees were documented near Nový Smokovec in the Tatra National Park. Photo: B. Konôpka.

ber 2004 occurred mainly at sites where similar events have been previously documented (Koreň 2005). It was connected with extremely strong wind, the velocity of which varied from 160 km h^{-1} in lower altitudes up to 200 km h^{-1} on mountain ridges (Kunca & Zúbrik 2006).

Another severe, large-scale wind disturbance in Slovakia was 15 May 2014. This partly overlapped in area with the November 2004 storm however, the affected area was smaller. In this particular case, the wind also damaged young pine and larch stands in planted forests (Fig. 4). Such damage can be explained by heavy rains which excessively saturated the soil, decreasing the stability of trees resulted in high numbers of locally uprooted or broken trees (Pajtík et al. 2015).

Direction, velocity and the effects of winds on forests in Slovakia can be related not only to synoptic-meteorological circumstances, but also the geography (diverse relief) of the western Carpathians (Konôpka J. et al. 2008). The relief determines varying exposition of forest stands to wind. The probability of wind damage to forest stands varies over the segmented relief. Generally, the more diverse the relief the more heterogeneous "behaviour" of the wind. In mountain areas, wind most frequently causes damage to forests in valleys, especially if the valleys follow the most dangerous wind direction and in places where the wind is funneled into a vally bend. Falling wind from mountain ridges accelerates fast (Stolina et al. 1985) and strong wind currents damage forests on the slopes and foothills.

In eastern Slovakia the prevailing direction of dangerous winds is from the north. In southwestern Slovakia, the most dangerous winds come from the northwest, followed by winds from the north and the west. In central Slovakia, heterogeneous relief means the direction of dangerous winds varies. However, considering Slovakia as a whole, southwesterly and northerly winds prevail (Konôpka J. et al. 2008).

In central Europe, the forests are exposed to dangerous winds, mainly in November, March and April (Stolina et al. 1985). Nearly half of the dangerous winds in Slovakia are recorded in winter (Konôpka B. & Konôpka J. 2009). Long-term analyses of meteorological records do not prove significant changes in frequency of dangerous winds compared to the past (Konôpka B. et al. 2010a). However, some modifications in seasonal distribution of dangerous winds exist (Fig. 5). Specifically, they include an increase in the number of dangerous windstorms in the spring and in contrast, a decrease in windstorms during the winter and summer. Further, changes in the direction of dangerous winds may be noticed, for example an increase in prevelance of the "traditional" nortwesterly winds (Table 1).

Table 1. Share of dangerous winds (velocity over 62 km h^{-1}) by direction (in percentages) over the period 1961–1990 and 1991–2010 in Slovakia (after B. Konôpka et al. 2010a, modified).

Period	N	NE	E	SE	S	SW	W	NW	Total
1961–1990	25	3	1	4	23	9	8	27	100
1991–2010	23	3	1	2	21	8	8	34	100

Explanations for main wind directions: N – north, NE – northeast, E – east, SE – southeast, S – south, SW – southwest, W – west, NW - northwest.

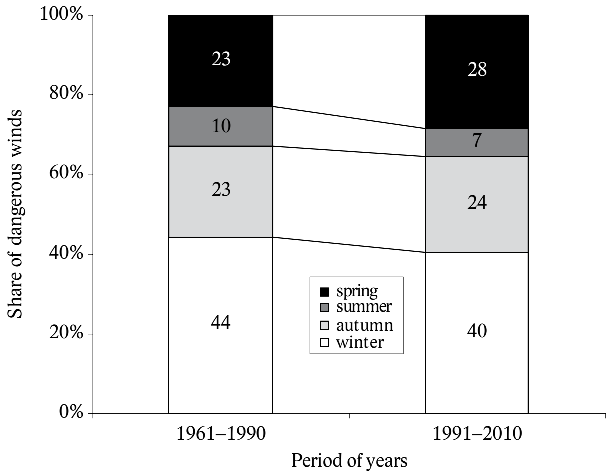

Fig. 5. Share of dangerous winds (velocity over 62 km h^{-1}) in Slovakia over the period 1961–1990 and 1991–2010 (after B. Konôpka et al. 2010a, modified).

Spruce stands in Slovakia are the most frequently damaged by wind in the northern and central regions (Konôpka B. & Konôpka J. 2009), namely in the regions of Orava, High Tatra and Low Tatra Mountains, Great Fatra Mountains, Pohronie, Poľana Mountains and Slovak Ore Mountains. Despite relatively good knowledge about spatial and temporal occurrence of dangerous winds, it is impossible to predict precisely the time, location and size of future wind disturbances in forests. Based on the extrapolation of the time series data on wind damage in the Slovak forests, it can be predicted that windstorms in this country will damage about 2.5 million m^3 of timber annually from 2016 to 2030 (Fig. 6). However, this is a rough estimate as damage to forests by wind will strongly depend on future weather which cannot be adequately predicted in the long-term.

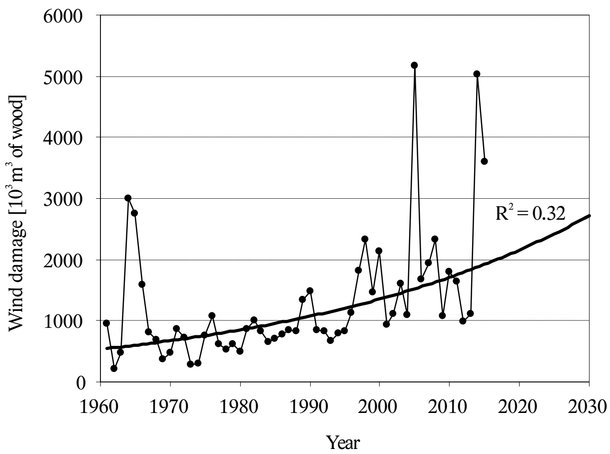

Fig. 6. Development of wind damage to forests in Slovakia between 1961 and 2015 in volumes of salvage felling (source: Forest Protection Service) and prediction up to 2030 as extrapolation by exponential function.

5. Conclusion

Wind is an important ecological factor affecting development, growth and reproduction of trees in forested ecosystems. Understanding interactions between wind and trees provides a baseline for prevention or mitigation of the negative impacts assocated with wind disturbances on forests worldwide. Forest destruction by wind and/or other harmful agents is a complex interaction, negatively influencing carbon reserves. The loss of carbon stored in tree biomass and forest soil is apparent in forests disturbed by wind. Forest recovery, to the former situation is long, usually taking several decades.

Since stimulating effects of inherent phenomena of climate change on frequency and intensity of destructive events in forests are associated with changes in carbon balance, the relationships (cycle) can be described as a positive feedback system as follows: climate change → induced disturbances to forest ecosystems → stimulated climate change. In the case of wind disturbances, there are no direct or immediate effective measures to eliminate the associated risks. However, conclusions can be made in the case of bark beetles, as early processing and removal of wind damaged and/or infested timber may mitigate or locally eliminate the outbreak. Thus, integrated forest protection becomes very important part of the forestry in the conditions of global change. It is also important in terms of stabilizing forest ecosystem services, especially with regard to carbon sequestration.

Knowledge on wind disturbances show that integrated forest protection against strong winds and other harmful agents in forest ecosystems in Slovakia and, highly likely, in other countries within Europe, will become important in the near future in the light of predicted global change.

Acknowledgements

The research was supported by the project APVV-14-0086 from the Slovak Research and Development Agency in the Slovak Republic, the projects VEGA 2/0035/13 and VEGA 2/0052/15 and the project QJ1520006 of the Ministry of Agriculture of the Czech Republic. Dr. Jennifer Clear is acknowledged for valuable comments on the manuscript.

References

Baker, W., 1995: Long-term response of disturbance landscapes to human intervention and global change. Landscape Ecology, 10:143–159.

Barnes, B. V., Zak, D. R., Denton, S. R., Spurr, S. H., 1998: Forest Ecology. John Willey & Sons, New York, 775 p.

Belanger, J. H., Arbas, E. A., 1998: Behavioral strategies underlying pheromone-modulated flight in moths: lessons from simulation studies. Journal of Comparative Physiology A, 183:345–360.

Blennow, K., Olofsson, E., 2008: The probability of wind damage in forestry under a changed wind climate. Climate Change, 87: 347–360.

Blennow, K., Sallnäs, O., 2004: WINDA – a system of models for assessing the probability of wind damage to forest stands within a landscape. Ecological Modelling, 175:87–99.

Coutts, M. P., Grace, J., 1995: Wind and Trees. Cambridge University Press, Cambridge, 485 p.

Cremer, K. W., Borough, C. J., Mckinnell, E. H. and Carter, P. R., 1982: Effects of stocking and thinning on wind damage in plantations. New Zealand Journal of Forestry Science, 12:244–268.

Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J.et al., 2001: Climate change and forest disturbances. BioScience, 51:723–734.

Ennos, A.R., 1997: Wind as an ecological factor. Trends in Ecology and Evolution, 12: 108-111.

Gardiner, B. A., Schelhaas, M. J., Blennow, K., Orazio, Ch., Landmann, G.: Wind storms and forest losses. A brief history of the wind damage to European forests. European Forest Institute, Forest Research. Avaiable at: www.forestreserach.gov.uk; www.efi. int.

Gardiner, B. A., 1995: The interaction of wind and tree movement in forest canopies. In: Coutts, M. P. and Grace, J. (eds.): Wind and trees. Cambridge, Cambridge University Press, p. 41–59.

Gardiner, B. A., Quine, C. P., 2000: Management of forests to reduce the risk of abiotic damage, a review with particular reference to the effects of strong winds. Forest Ecology and Management, 135:261–277.

Gardiner, B., Berry, P., Moulia, B., 2016: Review: Wind impacts on plant growth, mechanics and damage. Plant Science, 245:1–25.

Grubb, T. C., Jr., 1975: Weather-dependent foraging behavior of some birds wintering in a deciduous woodland. The Condor, 77:175–182.

Hannah, P., Palutikof, J. P., Quine, C. P., 1995: Predicting wind speeds for forest areas in complex terrain. In: Coutts, M. P. and Grace, J. (eds.): Wind and trees, Cambridge: Cambridge University press, p. 113–132.

He, H. S., Mladenoff, D. J., Crow, T. R., 1999: Linking an ecosystem model and a landscape model to study forest species response to climate warming. Ecological Modelling, 114:213–233.

Jaffe, D., Cerundolo, B., Rickers, J., Stolzberg, R., Baklanov, A., 1995: Deposition of sulphate and heavy metals on the Kola peninsula. Science of the Total Environment, 160/161:127–134.

Kärvemo, S., 2010: Population dynamics of tree-killing bark beetles – a comparison of the European spruce bark beetle and the North American mountain pine beetle. Introductory Research Essay, No 10, Department of Ecology, SLU Uppsala, 23 p.

Konôpka, B., 2000: Nové poznatky o vplyve vetra na lesné ekosystémy. In: Zúbrik, M. (ed.): Aktuálne problémy v ochrane lesa 2000. Zvolen, LVÚ Zvolen, p. 23–28.

Konôpka, B., 2007: Potenciálne riziká vplyvu klimatickej zmeny na les; hypotézy, výskum a perspektívy. Lesnícky časopis - Forestry Journal, 53:201–213.

Konôpka, B., Konôpka, J., 2003: Static stability of forest stands in the seventh altitudinal vegetation zone in Slovakia. Journal of Forest Science, 49:474–481.

Konôpka, B., Konôpka, J., 2009: Vietor a sneh – najzávažnejšie abiotické škodlivé činitele. Zvolen, NLC, 11 p.

Konôpka, B., Konôpka, J., Raši, R., Nikolov, Ch., 2010a: Zhodnotenie smerov nebezpečného vetra pre lesné porasty na Slovensku v období rokov 1961–2005. Acta Facultatis Forestalis, 52: 63–74.

Konôpka, B., Moravčík, M., Pajtík, J., Lukac, M., 2010b: Effects of soil waterlogging on below-ground biomass allometric relations in Norway spruce. Plant Biosystems, 114:448–457.

Konôpka, B., Konôpka J., Vakula J., 2011: Vietor, sneh a podkôrny hmyz – najzávažnejšie škodlivé činitele v lesoch Slovenska. In: Kunca, A. (ed): Aktuálne problémy v ochrane lesa 2011. Zvolen, NLC, p. 82–88.

Konôpka, J., 1977: Vplyv rastových vlastností smreka na odolnosť lesných porastov proti vetru v oblasti Nízkych Tatier. Poľnohospodárska veda No. 1, Bratislava, 172 p.

Konôpka, J., Konôpka, B., Raši, R., Nikolov, Ch., 2008: Nebezpečné smery vetra na Slovensku. Lesnícke štúdie, 60, Zvolen, NLC, 81 p.

Koreň, M., 2005: Vetrová kalamita z 19. novembra 2004 – nové pohľady a konzekvencie. Tatry, 44:6–29.

Kozlowski, T. T., Kramer, P. J., Pallardy, S. G., 1991: The Physiological Ecology of Woody Plants. San Diego, Academic Press, 657 p.

Krippel, E., 1965: Postglaciálny vývoj lesov Záhorskej nížiny (Historicko-geobotanická štúdia). Biologické práce SAV, 5:1–33.

Kunca, A., Zúbrik, M., 2006: Vetrová kalamita z 19. novembra 2004. Zvolen, NLC, 40 p.

Kunca, A., Zúbrik, M., Galko, J., Vakula, J., Leontovyč, R., Konôpka, B.et al., 2015: Salvage felling in the Slovak forests in the period 2004–2013. Lesnícky časopis - Forestry Journal, 61:188–195.

Lässig, R., Schönenberger, W., 2000: Nach Lothar und Vivian-Erfahrungen profitieren. Wald und Holz, 81:31–35.

Letelier, M. F. S., Valdivia, J. M., Leutheusser, H. J., 1988: An analytical model of the wind-induced spread of forest fires. Journal of Wind Engineering and Industrial Aerodynamics, 30:215–219.

Matsuzaki, T.,1994: Impact of wind and snow on forest. In: Proceedings of NAFRQ seminar on sustainable forestry and its biological environment. Tokyo: Japan Society of Forest Planning Press, p. 145–148.

Mitchell, S. J., 2013: Wind as a natural disturbance agent in forests: a synthesis. Forestry – an International Journal of Forest Research, 86:147–157.

Nikolov, Ch., Barka, I., Ferenčík. J., Hlásny, T., Vakula, J., Zúbrik, M. et al., 2010: Využitie geografických informačných systémov a diaľkového prieskumu Zeme pre hodnotenie zmien stavu lesa po roku 2004 vo Vysokých Tatrách. In: Konôpka, B. (ed): Výskum smrečín destabilizovaných škodlivými činiteľmi. Zvolen, NLC, p., 96–106.

Nikolov, Ch., Konôpka, B., Kajba, M., Galko, J., Kunca, A., Janský, L., 2014: Post-disaster Forest Management and Bark Beetle Outbreak in Tatra National Park, Slovakia. Mountain Research and Development, 34:326–335.

Odum, E. P., 1983: Basic Ecology. CBS College Publishing, Holt, Rinehart and Wiston, The Dryden Press, 613 p.

Pajtík, J., Konôpka, B., Šebeň, V., Michelčík, P., Fleischer, P., 2015: Alokácia biomasy smrekovca opadavého prvého vekového stupňa vo Vysokých Tatrách. Štúdie o Tatranskom národnom parku, 11:237–249.

Peltola, H., Kellomaki, S., Vaisanen, H., Ikonen, U. P., 1999: A mechanistic model for assessing the risk of wind and snow damage to a single tree and stands of Scots pine, Norway spruce and birch. Canadian Journal of Forest Research, 29:261–267.

Peltola, H., Ketlomaki, S., Kolstrom, T., Lassig, R., Moor, J., Quine, C. et al., 2000: Wind and other abiotic risks to forests. Forest Ecology and Management, 135:1–2.

Quine, C. P., 2003: Wind-driven gap formation and gap expansion in spruce forest of upland Britain. In: Ruck, B., Kottmeier, C., Matteck, C., Quine, C., Wilhelm, G. (eds.): Proceedings of the International Conference Wind Effects on Trees. Published by Lab Building, Environment Aerodynamics, Institute of Hydrology, University of Karlsruhe, Germany, p. 101–108.

Raffa, K., Aukema, B., Bentz, B., Carroll, A., Hicke, J., Turner, M., et al., 2008: Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience, 58: 501–517.

Robertson, C., Wulder, M. A., Nelson, T.A., White, J., 2009: Preliminary risk rating for mountain pine beetle infestation of lodgpole pine forests over large areas with ordinal regression modelling. MBB Working Paper 2009-19, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, 24 p.

Schelhaas, M. J., Nabuurs, G. J., Sonntag, M., Pussinen, A., 2002: Adding natural disturbances to a large scale forest scenario model and a case study for Switzerland. Forest Ecology and Management, 167:13–26.

Schelhaas, M. J., Nabuurs, G. J., Schuck, A., 2003a: Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology, 9:1620–1633.

Schelhaas, M. J., Schuck, A., Varis, S., 2003b: Database on forest disturbances in Europe (DFDE) – technical description. EFI Internal Report, 14:2–44.

Schindler, D., Bauhus, J., Mayer, H., 2012: Wind effects on trees. European Journal of Forest Research, 131:159–163.

Schönenberger, W., 2002: Windthrow research after the 1990 storm Vivian in Switzerland: objectives, study sites, and projects. Forest Snow Landscape Research, 77:9–16.

Skuhravý, V., 2002: Lýkožrout smrkový *Ips typographus* (L.) a jeho kalamity. Agrospoj, s.r.o., Těšnov, Praha, 196 p.

Stolina, M. et al., 1985: Ochrana lesa. Bratislava, Príroda, 473 p.

Svoboda, M., Janda, P., Bače, R., Fraver, S., Nagel, T. A., Rejzek, J. et al., 2014: Landscape-level variability in historical disturbance in primary *Picea abies* mountain forests of the Eastern Carpathians, Romania. Journal of Vegetation Sciences, 25:386–401.

Valinger, E., Lundqvist, L., Bondesson, L., 1993: Assessing the risk of snow and wind damage from tree physical characteristics. Forestry, 86:249–260.

Vančura, K., Raben, G., Gorzelak, A., Mikulowski, M., Čaboun, V., Oleksyn, J., 2000: Impact of air pollution on the forests of central and eastern Europe. In: Innes, J. L., Oleksyn, J. (eds.): Forest dynamics in heavily polluted regions. Report No. 1 of the IUFRO task force on environmental change, CABI Publishing and IUFRO, Oxon, New York, p. 121–146.

Zach, P., Kršiak, B., Kulfan, J., Cicák, A., Krištín, A., Váľka, J., Vargová, K., 2009: Dynamika podkôrnikovitých (Coleoptera: Scolytidae) v horskom smrekovom lese Tatier ovplyvnenom vetrovou kalamitou: lykožrút smrekový *Ips typographus* (L.) a lykožrút lesklý *Pityogenes chalcographus* (L.). In: Tužinský, L., Gregor, J. (eds.): Vplyv vetrovej kalamity na vývoj lesných porastov vo vysokých Tatrách. Zvolen, Technická univerzita vo Zvolene, 165–172.

Zach, P., Kršiak, B., Kulfan, J., Holecová, M., 2010: Attraction of bark beetles (Coleoptera: Scolytidae) to Norway spruce in timberline forest in Tatra Mountains, West Carpathians. Lesnícky časopis - Forestry Journal, 56:285–293.

Zach, P., Kršiak, B., Kulfan, J., 2015: Desať rokov výskumu dynamiky podkôrnikovitých (Coleoptera. Curculionidae, Scolytinae) po veternej disturbancii v Tichej doline v Tatrách. Štúdie o Tatranskom národnom parku, 11:331–339.

Zach, P., Kršiak, B., Kulfan, J., Parák, M., Kontschán, J., 2016: Mites *Trichouropoda* and *Uroobovella* spp. (Uropodoidea) phoretic on bark beetles (Scolytinae): a comparison from a declining mountain spruce forest in Central Europe. International Journal of Acarology, 42:212–217.

Wermelinger, B., 2004: Ecology and management of the spruce bark beetle *Ips typographus* – a review of recent research. Forest Ecology and Management, 202:67–82.

Westfall, J., 2007: Summary of forest health conditions in British Columbia. Ministry of Forests, Forest Practices Branch, Vicroria, BC, 66 p.

White, P. S., Pickett, S. T. A., 1985: Natural disturbance and patch dynamics: an introduction. In: Pickett, S. T. A., White, P. S. (eds.): The ecology of natural disturbance and patch dynamics, Academic Press, New York, p. 3–13.

Wyatt, T. D., 2003: Pheromones and animal behaviour: communication by smell and taste. Cambridge University Press, Cambridge, 393 p.

Zeng, H., Gonzalo, J. G., Peltola, H., Kellomäki, S., 2010: The effects of forest structure on the risk of wind damage at a landscape level in a boreal forest ecosystem. Annals of Forest Science, 67:64–72.

Zhu, J. J., Gonda, Y., Matsuzaki, T., Yamamoto, M., 2002b: Salt distribution in response to optical stratification porosity and relative windspeed in a coastal forest in Niigata. Agroforestry Systems, 56:73–85.

Zhu, J. J., Matsuzaki, T., Li, F. Q., Gonda, Y., 2002a: Theoretical derivation of risk-ratios for assessing wind damage in a coastal forest. Journal of Forestry Research, 13:309–315.

Zhu, J. J., Liu, Z. G., Li, X. F., Takeshi, M., Yutaka, G., 2004: Review: effects of wind on trees. Journal of Forestry Research, 15:153–160.