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Quantification of time delay between damages caused by windstorms and by *Ips typographus*

Kvantifikace časového odstupu mezi škodami větrem a *Ips typographus*

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Abstract

Damages by wind and by European spruce bark beetle (*I. typographus* L.) were compared on the basis of the reports about the occurrence of harmful forest agents for the period 1964−1991 across former regional state forest directorates. In the given period, the quantity of salvage logging (70 million m^3) was more than five times that of sanitation felling (13 million m^3). Damage intensity increased over the decades. Using a cross-correlation function between the time series, an increase in the abundance of *I. typographus* due to windfall was demonstrated with a delay of 1–3 years. Wind damage was also shown to arise as a result of disturbed stand stability after sanitation felling with a stochastic delay of 1−5 years. Thus, disturbance of static stability of forest stands may be considered as one of the main harmful consequences of bark beetle outbreaks for the near future. Consequences for forest management are discussed.

Key words: forest pest management; disturbance; windfall; bark beetles; population dynamics

Abstrakt

Na základě hlášení o výskytu lesních škodlivých činitelů za období 1964−1991 byly na úrovni tehdejších krajských ředitelství státních lesů porovnávány škody větrem a lýkožroutem smrkovým − *Ips typographus* [L.]. V daném období představovala nahodilá těžba vlivem větru (70 mil. m^3) více než pětinásobek kůrovcových těžeb (13 mil. m^3). Mezi jednotlivými dekádami docházelo k nárůstu intenzity škod. Pomocí křížové korelační funkce mezi časovými řadami bylo prokázáno zvýšení početnosti *I. typographus* následkem větrných polomů se zpožděním 1−3 roky, ale také vznik škod větrem jako následek porušení stability porostů po kůrovcových těžbách se stochastickým zpožděním 1−5 let. Porušení statické stability lesních porostů může tak být v blízké budoucnosti považováno za jeden z hlavních škodlivých následků kůrovcových kalamit. Důsledky pro lesnické hospodaření jsou diskutovány.

Klíčová slova: ochrana lesa; disturbance; polom; kůrovci; populační dynamika

1. Introduction

The vast majority of forests in the Czech Republic are today markedly influenced by direct and indirect human interventions. Original natural forest climax ecosystems with high diversity have been gradually reduced or transformed to mostly even-aged stands with greater than 50% representation of Norway spruce (*Picea abies* [L.] Karst). Moreover, current spruce stands are largely located in uplands where precipitation totals are lower than this tree species requires over the long term. Forest stands are therefore under long-term stress and are losing their ability to sufficiently protect themselves against the activation of harmful agents by means of their own internal auto-regulatory mechanisms (Jančařík 1998). In connection with manifestations of the current phase of long-term climatic changes, a growing number of authors (Schelhaas et al. 2003; Lindner et al. 2010) have agreed that extreme meteorological events including the frequency and strength of wind storms will increase, which will significantly affect forest management.

Not only does incidental logging caused by abiotic and biotic factors represent financial losses in planned forest management, it also complicates the efforts to rapidly transform the species composition of forests and to shift toward close-to-nature forestry. During 1960–1985s, approximately 30% of the total annual logging in Czech lands could be attributed to harmful agents, while in disaster periods this share increased to 90% (Peřina 1987). Given the species composition of Czech forests, the most significant causes of incidental logging are strong winds (combined with snow and rime they make up to 80% of incidental logging) and bark-boring insects on spruce. Large disturbances caused by abiotic agents are typically one of the frequent causes of subsequent outbreaks of bark-boring (Wermelinger 2004; Stadelmann et al. 2013) or other insects (Hanewinkel et al. 2008).

During bark beetle outbreaks in the 19th and 20th centuries, more than 30 million m^3 of wood was logged (Skuhravý 2002). The European spruce bark beetle *Ips typographus* (Linnaeus, 1758) is considered one of the most significant bark-boring insect species damaging forest stands over the long term (Christiansen & Bakke 1988). Spruce trees 70–100 years of age (Netherer & Nopp-Mayr 2005) exposed to the south and west (Wermelinger 2004) are particularly at risk. Mass attacks of this pest are mediated by semiochemicals, with a direct relationship existing between tree resistance and its successful infestation (Raffa & Berryman 1983; Christiansen et al. 1987).

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In terms of damage, the crucial aspect is *I. typographus* population dynamics, which is influenced by numerous factors that are very difficult to describe as a whole. Individual outbreaks have almost constant duration, while the length of the inter-generation period is highly variable (Økland & Bjornstad 2006). This fact is based also on the existence of two possible, alternatively occurring sources of material suitable for larval development. Under usual conditions, living (probably weakened) standing trees are infested. If wind damage occurs, however, fallen trees are the predominant development substrate.

Windfall is an easily colonisable but transient resource, while the possibility of infesting standing trees depends mainly on their physiological state (resistance) and on the local bark beetle population density (Christiansen et al. 1987). There are two levels of bark beetle population density – non-epidemic (K_1) and epidemic (K_2), or rather two carrying capacities for trophically different environments. The carrying capacity of an environment is considered to be the value corresponding to the highest achievable population density within an inhabited space that a population can reach without unfavourably impacting the ecosystem and thereby limiting the living conditions of its members. At a low number of bark beetles (latent period), most standing trees are sufficiently resistant to infestation. With the increasing duration of inter-gradation periods, the proportion of physiologically weakened and dying trees in stands naturally increases (Økland & Bjørnstad 2006). As long as these resources are "relatively rare" (carrying capacity K_1), they are subject to competition and the bark beetle population is maintained by negative feedback at a balanced (low) population density. At a certain unstable moment (so-called threshold value K_3), however, bark beetle abundance increases to such an extent that it enables the cooperation among beetles to overcome the resistance of standing vital trees and colonise previously inaccessible resource (Berryman & Kindlmann 2008). An ever increasing bark beetle population density, however, gradually reaches the epidemic level of the environment's carrying capacity K_2 and again causes increased competition for available space for offspring development. Upon exhaustion of the short-term above-standard supply during outbreak, bark beetle density stabilises at carrying capacity K_1 corresponding to the environment's usual supply (Berryman & Kindlmann 2008).

The population dynamics of *I. typographus* may therefore be characterised as eruptively pulsating (Berryman 1987) with considerably delayed negative feedback. Disturbance processes play a key role in the shift between endemic and epidemic population densities (Kausrud et al. 2012). An outbreak usually lasts 3–11 years (Skuhravý 2002), or 5–7 years (Sauvard 2004), during which large numbers of trees die due to infestation (Sauvard 2004). In Central Europe, wind disturbances are the most significant events (Schelhaas et al. 2003) able to synchronise the population dynamics of *I. typographus* over broad areas (Økland & Bjørnstad 2006). Bark beetle population density increases with a certain delay after a windstorm damage event. The infestation of standing trees is minimal in the first vegetation season following wind disturbance (Schroeder 2001; Grodzki et al. 2010; Stadelmann et al. 2014). In Norway, Økland & Berryman (2004) observed an increase in bark beetle population densities 1 year after a windfall event. According to Wermelinger & Seifert (1999), population density in the Swiss Alps showed the largest growth 2 years after the occurrence of extensive windfalls. Based on long-term data from the Polish Tatras, Grodzki & Guzik (2009) also stated a 2-year interval. From southern Sweden, Schroeder & Lindelöw (2002) reported a peak in the increase of sanitation felling in the second and third years after a windfall event. In certain areas, e.g. in the Bavarian Forest, a peak in the increase of infested trees was recorded in the fourth and fifth years after the occurrence of windfall (Schroeder 2001). In the Czech Republic, Skuhravý (2002) reported that substantial increases in *I. typographus* population density frequently occur in the first year following wind disturbance. In forestry practice, however, the generally prevailing opinion is that there is a dominantly 2-year shift.

Although quite satisfactory data as to the harmful effects of wind and bark beetles on spruce exist for the territory of the Czech Republic, difficulties arise when trying to obtain representative data for a long time period from a specific region. Compiled historic disaster overviews (Kudela 1946, 1980, 1984; Jančařík 1998) have included only the most important events. Continuous data about the amount of salvage logging and sanitation felling as of 1985 were published by Peřina (1987) and Liška et al. (1991), but only for the entire Czech territory. Another available summary resources for the Czech lands are statistical yearbooks in which damages caused by wind are, however, indicated together with those caused by other abiotic influences (e.g. snow and rime), and damages caused by *I. typographus* are recorded together with those of other spruce bark beetle species.

The objective of the present study is to create an overview of incidental loggings caused by wind and by European spruce bark beetle in the Czech lands over the period 1964–1991 at a level of the former regional divisions of the Czech state forests and analyse the data. This study used the information from the annual reports on the incidence of harmful forest agents (so called L116 form). The main task was to characterise the time delay between damages caused by wind and by *I. typographus*, as well as the time delay between sanitation felling and salvage logging.

2. Materials and methods

The mean elevation of the Czech Republic (78,867 km^2) is 430 m a.s.l., while 5% of the state's area is below 200 m a.s.l., 74.1% is between 201 and 600 m a.s.l., 19.3% is between 601 and 1,000 m a.s.l., and 1.6% is above 1,000 m a.s.l. (Bína & Demek 2012). The climate is mildly humid with annual precipitation totals of 450–1,200 mm and average annual air temperature of 2°C to 10°C (Tolasz et al. 2007). Table 1 presents the characteristics of the natural conditions of the former regional divisions within the Czech lands. From a phytogeographic perspective, the Czech territory belongs to the vegetation belt of broadleaf deciduous forests characterised by a short developmental cycle in which no stage of large-area disturbances related to the creation of large-area gaps naturally occurs. This differentiates these forests from the more northerly located belt of boreal coniferous forests characterised by a long developmental cycle and where large-scale disturbances of stands are considered common (Míchal 1994; Poleno et al. 2007). The natural share of conifers was reconstructed at 34.7% and of broadleaf trees at 65.3%. The current representation is 72.9% conifers and 25.9% broadleaves. The share of Norway spruce in the natural species composition was 11.2%, while currently it stands at 51.1%. Its share has been gradually decreasing in recent years due to targeted forestry interventions (Report 2015). The area of forests in the Czech lands gradually grew from 2,463,000 ha in 1960 to 2,578,000 ha in 1985, while the proportion of spruce decreased from 60.5% in 1950 to 55.5% in 1985 (Peřina 1987).

The data from the period 1964–1991 were used to compare the damage caused by wind and by *I. typographus*. Annual reports on the incidence of harmful agents submitted by forestry enterprises of what was then the Czechoslovak State Forests for individual forest districts on unified L116 forms are available from the Forest Protection Services' archive (FGMRI) for the given time period. L116 forms became valid in 1964 and remained valid and unchanged until 1991. After 1991, national forests underwent a change in configuration connected with the restitution of forest properties, due to which data were no longer collected using this form. Although the Czechoslovak State Forests did not own all forests, only 3% of forests in 1960 and 0.09% in 1985 were private forests (Peřina 1987). Thus, professional management and collection of data about the occurrence of harmful agents were carried out by the Czechoslovak State Forests. Some forms, however, have not been preserved in the archive to this day, and thus the smallest areas with separate forest registries cannot be used for the intended comparison. Nevertheless, the summary data from the regional forest state directorates were preserved, with the sole exception of the corporate directory of Vojenské lesy a statky (Military Forests and Farms) which was under the management of the Ministry of Defence. The smallest usable units with the complete data covering the entire Czech Republic today are therefore the former regional state forest directorates, of which 7 were located within the Czech lands during 1964–1991 (Bluďovský 1985; see Table 1).

The L116 reports were submitted every calendar year. Wind damage (without further differentiation) and commonly registered damages caused by *I. typographus* and *I. amitinus* (Eichhoff, 1871), including the volume of trap trees, were stated in m^3. Other spruce bark beetles, mainly *Pityogenes chalcographus* (Linnaeus, 1761), were reported separately from *I. typographus* and *I. amitinus*, and were not included in the study. According to Liška et al. (1991), the long-term share of other bark beetle species in the total volume of spruce wood infested by bark-boring insects in the Czech lands was less than 7%. Therefore, the amount of wood infested by *I. amitinus* may be regarded as negligible for the monitored period and the volume of reported damages may essentially be attributed to the main species, *I. typographus*. Therefore, the European spruce bark beetle is reported in the following text as the sole originator of all reported damages. In keeping with the efforts to unify the use of terminology (Stadelmann et al. 2013), the present study uses the terms "salvage logging" for logging of wood due to wind damage and "sanitation felling" for logging of trees infested by *I. typographus*. In the case of sanitation felling, however, the author's definition could not be diligently followed as the share of trap trees was not separately stated in the L116 reports. This unknown volume of trap trees would otherwise be deducted from the sanitation felling figure if the terminological purity is to be ensured.

We used a cross-correlation function that allows the identification of delay (mutual shift) of one time series against another (StatSoft 2013) to describe and model the relationship between damages caused by wind and by *I. typographus*. The significance of the shift was considered at a significance level $\alpha = 0.05$. We used the software Statistica 10.0 Cz to display and calculate the cross-correlations and to model the shifts.

3. Results

An overview of damages caused by wind and by bark beetles in particular forest state directorates is recorded in Figure 1. The most significant wind episodes were registered in 1967, 1976, 1984, and 1990. The total volume of windfall occurring in these four years comprised more than 30% of all windfall events over the entire monitored period of 28 years. The aggregated data for the Czech territory demonstrate gradually increasing quantities of logged wood damaged by wind. The area of the North Moravian State Forests has a different character of wind damages as compared to others. The wind there had an enduringly higher intensity of influence but maximum logging amounts were not achieved during significant wind events. The lowest wind damage was reported by the Central Bohemian State Forests directorate.

Table 1. General characteristics of individual directorates of Czech state forests. Forest area and forest cover were taken from Němec (1964), and proportion of spruce from Annonymous (1971), mean elevation, mean annual temperature and mean annual precipitation were derived from Annonymous (1972).

	Forest area [thous ha]	Forest cover [%]	Proportion of spruce [%]	Mean elevation [m a.s.l.]	Mean annual temperature [°C]	Mean annual precipitation [mm]
Central Bohemian State Forests Benešov	291.2	25.4	38.9	250–500	8–9	500–600
South Bohemian State Forests České Budějovice	387.4	34.1	53.4	600–900	5–8	700–1,000
West Bohemian State Forests Plzeň	419.5	38.6	63.1	500–800	5–8	600–1,100
North Bohemian State Forests Teplice	262.5	33.6	56.2	300–700	4–9	450–1,300
East Bohemian State Forests Hradec Králové	327.4	29.1	66.0	300–1,000	4–9	700–1,200
South Moravian State Forests Brno	427.5	28.5	43.6	300–600	7–10	500–600
North Moravian State Forests Krnov	393.7	35.6	65.6	400–900	5–9	700–1,300
Czech Republic	2,509.2	31.8	56.0	400–500	6–8	450–1,200

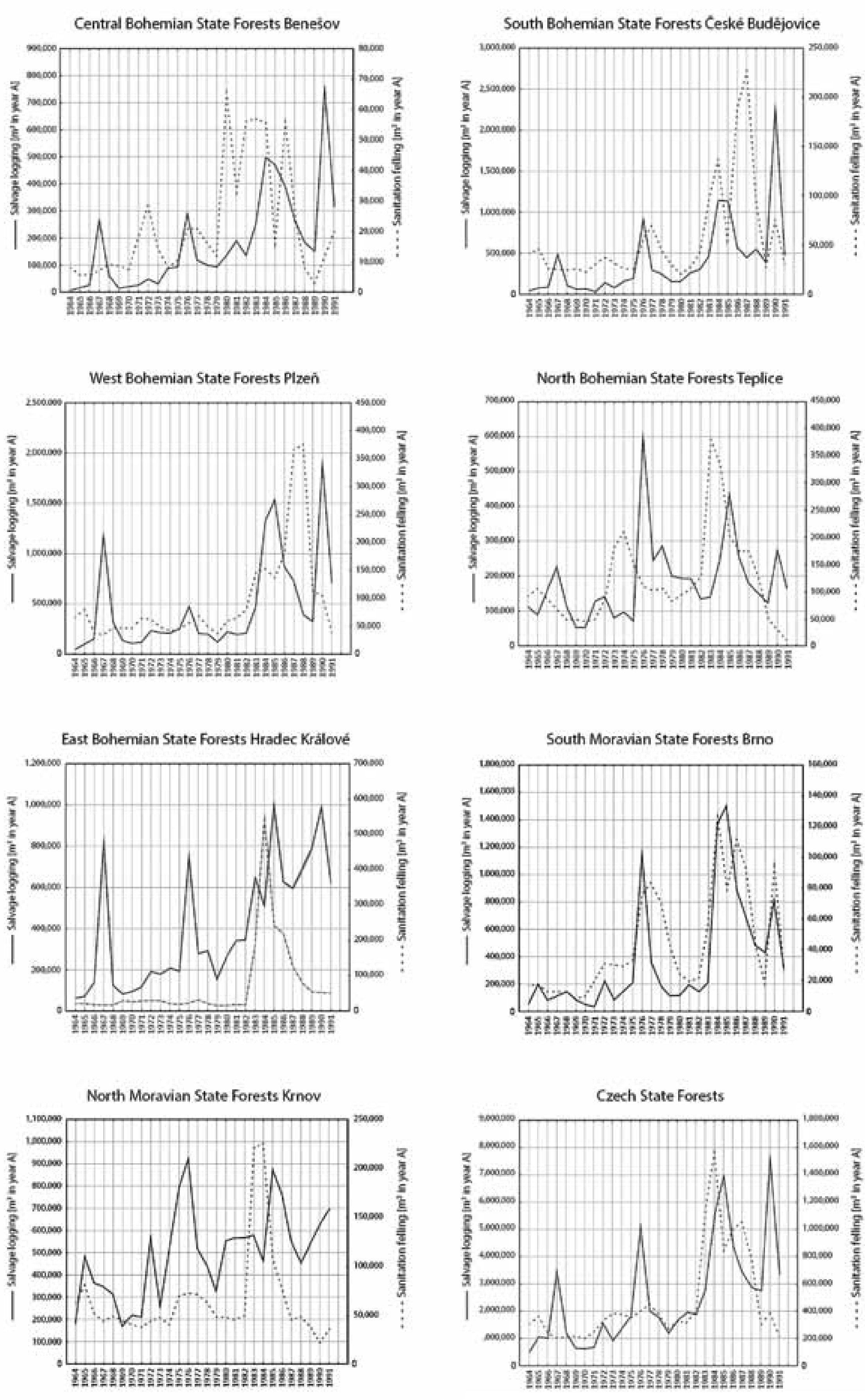

Fig. 1. Salvage logging and sanitation felling in individual regions of today's Czech Republic, 1964–1991.

European spruce bark beetle outbreaks are less synchronised than wind damage (Fig. 1). Regionally coincident gradation of the bark beetles within the majority of the area occurred only in the mid-1980s. The individual peaks of the calamity occurrence curves usually have a convex shape, demonstrating gradual onset and abatement of outbreak. The year 1984 in the North and East Bohemia and the year 1987 in the West Bohemia fall outside of this pattern, as at that time enormous year-on-year increases in sanitation felling occurred in those areas. It can be said that before 1980 the occurrence of bark beetles on spruce was relatively stable, while the 1980s represent a period of marked outbreaks. The culmination point of sanitation felling for the Czech state forests as a whole (Fig. 1) shown in 1984 apparently exceeds the peak of wind damage, but it is necessary to account for the different scales of the two types of damages (e.g. in 1990 a five-fold difference).

Table 2 presents the calculated cross-correlation coefficients for different time delays between salvage logging and sanitation felling which were statistically significant. Zero shifts were significant in two regions. In the South Moravia, sanitation felling volumes very closely mirrored windfall volumes (Fig. 1), which also corresponds with the strong cross-correlation (r = 0.79). The increases in the volume of wood infested by bark beetle with 1- to 3-year delays after windstorm disturbance were observed in four regions. Figure 2 depicts the most important relationships. In contrast, a significant shift in wind damage after sanitation felling with a delay of 1–5 years was found in six regions. It may be assumed that sanitation felling results in the exposure of previously protected stand edges to strong winds, which in turn leads to windfall events in these locations. Figure 3 depicts the most important shifts. A significant zero shift and an increase in wind damage after sanitation felling with a delay of 1–3 years were recorded for the Czech State forests as a whole (Table 2).

4. Discussion

Several crucial wind episodes with a nationwide effect, and usually extending beyond the Czech borders, had a marked influence on the total volume of wood logged in the studied period. The North Moravian Region represents an exception, as the volume of salvage logging from local wind storms was high during the entire monitored period but did not reach the maximum values in those years when the major wind damages affecting the entire Czech territory occurred. This fact is surprising as, in addition to the Jeseníky Mountains, the windiest places in the Czech lands are located in the Krkonoše Mountains, in the Ore Mountains at elevations above 800 m a.s.l., and in the Central Bohemian Uplands (Tolasz et al. 2007). The causes of consistently high salvage logging in the North Moravian Region cannot be easily determined. It may be assumed, however, that it reflects a combined effect of several influences. One possible explanation may be the

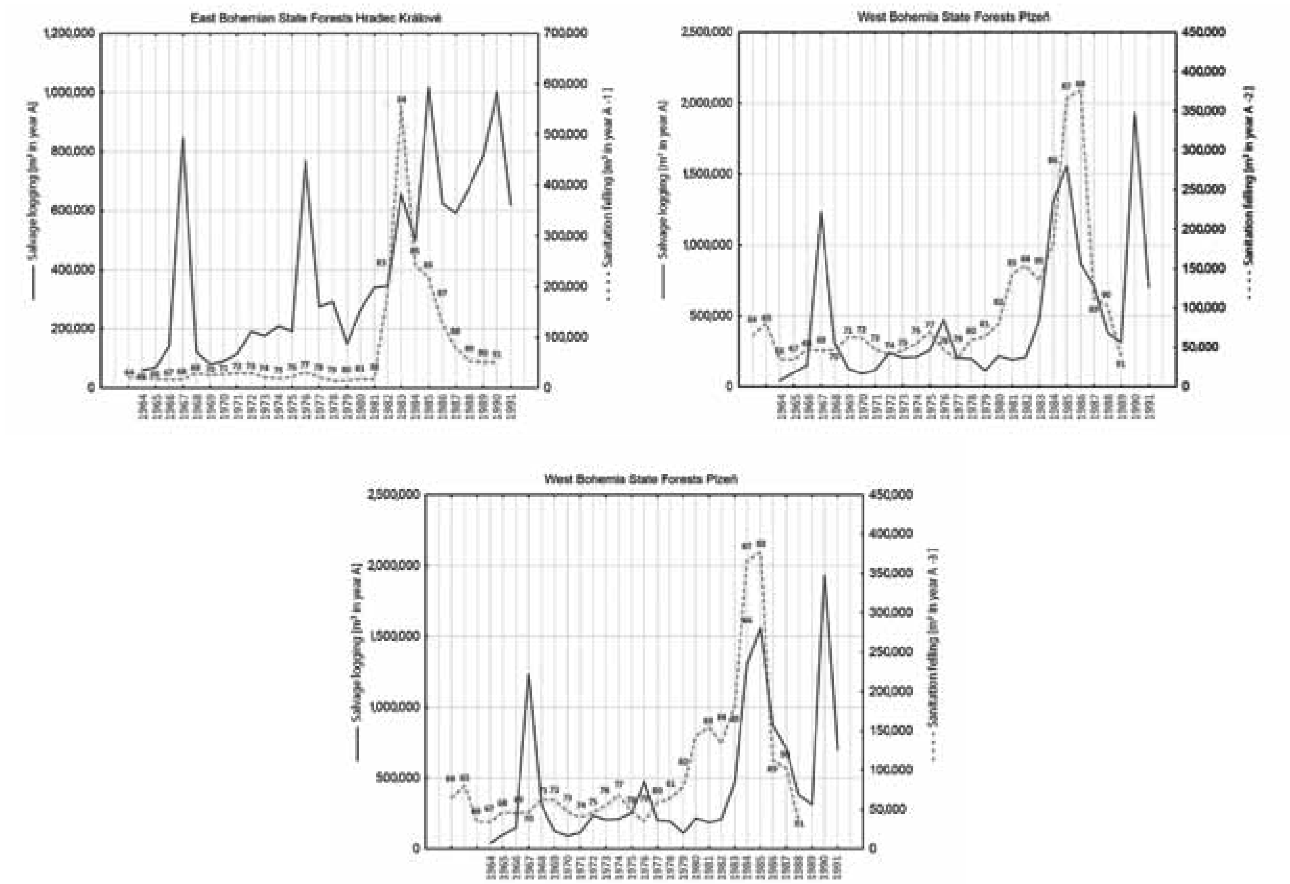

Fig. 2. Most important shifts in sanitation felling after salvage logging during 1964−1991, with time delays of 1–year, 2–years and 3–years.

Table 2. Significant cross-correlations for different time delays between regional volumes of salvage logging and sanitation felling.

	Sanitation felling after windstorm damages					Salvage logging after bark beetle outbreaks				
Time delay [year]	4	3	2	1	0	1	2	3	4	5
Central Bohemian State Forests Benešov	—	—	—	—	—	—	—	0.42	0.72	—
South Bohemian State Forests České Budějovice	—	—	0.46	—	—	—	—	0.54	0.43	—
West Bohemian State Forests Plzeň	—	0.56	0.54	—	—	—	0.53	0.51	—	—
North Bohemian State Forests Teplice	—	—	—	—	—	—	0.54	—	—	—
East Bohemian State Forests Hradec Králové	—	—	—	0.38	0.37	0.52	0.39	—	0.41	0.42
South Moravian State Forests Brno	—	—	0.46	0.57	0.79	0.51	—	—	—	—
North Moravian State Forests Krnov	—	—	—	—	—	—	—	—	—	—
Czech Republic	—	—	—	—	0.52	0.57	0.55	0.42	—	—

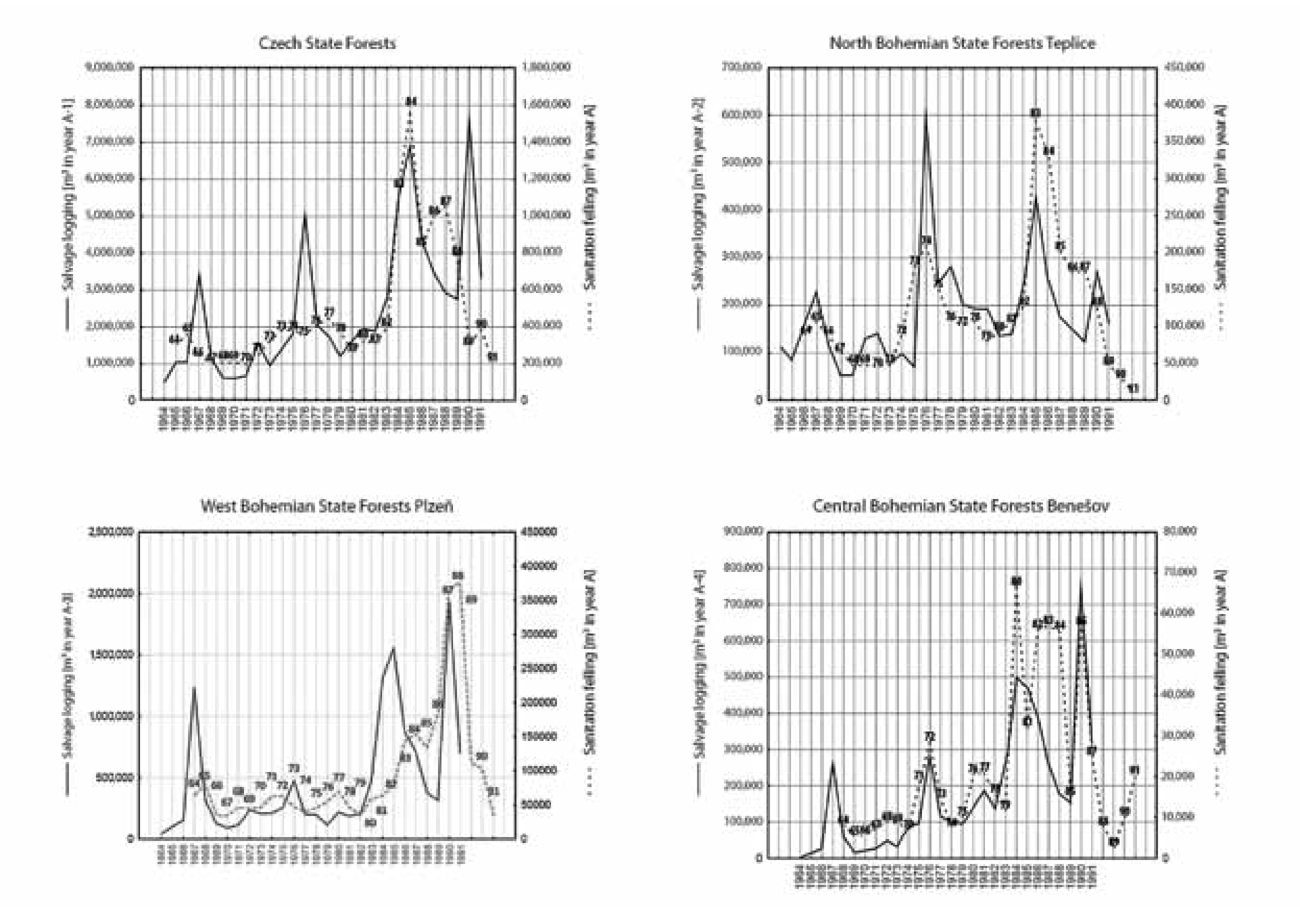

Fig. 3. Most important shifts in salvage logging after sanitation felling during 1964–1991, with time delays of 1–year, 2–years, 3–years and 4-years.

relatively heterogeneous structure of the local stands, which increases the frequency of windfall while at the same time decreasing its extent.

The generally observed trend in Europe of an increase in the frequency and rate of wind damage to forest stands (Schelhaas et al. 2003) may also be confirmed at the Czech territory for the monitored period. The causes of this trend have yet to be satisfactorily explained. Some authors point to the effect of global climate change (Schwierz et al. 2010) or changes in forest stand management (Schelhaas et al. 2003). Prolonging the rotation period with the objective of increasing the production of thicker-diameter wood, which has also been observed in the Czech territory (cf. Peřina 1987), causes an imbalanced representation of age classes favouring older trees. Older trees are taller and become more vulnerable to the effects of strong wind (Valinger & Fridman 2011). Schelhaas et al. (2003) consider the changes in forest management practices directed toward close-to-nature management as the most probable explanation of increasing forest stand wind damage. In the Czech lands, the shift to close-to-nature management was connected especially with a gradual decrease in spruce representation (cf. Peřina 1987) and with a decrease in the maximum permitted size of clearcutting. It is difficult to assess the direct impact of these measures as such changes take place over several decades. Nevertheless, they are expected to have a rather favourable influence. Air pollution can be another factor that could also influence the increase in the volume of salvage logging especially in the North Bohemia. According to Lekeš & Dandul (2000), pollutants damage root systems, thereby increasing tree instability.

The increasing frequency of strong winds in the Czech territory between 1500 and the present day has been documented by Dobrovolný & Brázdil (2003). The records furthermore show that damaging events have greatly accelerated in recent decades, although this does not correspond with the data acquired in the past. It is important to note that the records from earlier periods were sparse, and only later they began to be collected systematically. The increase in the number of wind storms may therefore be attributed to an increasing number of recorded events (Schelhaas et al. 2003). In this regard, the L116 reports were prepared according to the same methodology over the entire monitored period and thus the data are a relatively consistent time series.

In accordance with the findings of Dobrovolný & Brázdil (2003), a gradual increase in the maximum wind speed for the period 1950–2008 was also demonstrated in Switzerland (Brönnimann et al. 2012). Over a similar time span of 1958–2007, forest stand damage in Switzerland was 17 times greater than in the period 1908–1957 and 22 times greater than during 1858–1907 (Usbeck et al. 2010). The connection with the climate change appears to be more apparent when accounting for the fact that wind damage to forest stands occurred in 96% of cases at times when the soil was wet and not frozen. Moreover, the average winter temperature increased by 2°C during the monitored period and total winter precipitation by almost 50% (Usbeck et al. 2010). Similarly, in the Czech lands, wind storms damaging forest stands mostly occur in winter (Vicena et al. 1979).

The development of sanitation felling during the period 1964–1991 can be divided into two stages. In the first stage (1964–1979), only smaller regional outbreaks of primarily *I. typographus* occurred. In the second stage (1980–1991), the weakening of stands by pollutants probably started to have an effect, additionally reinforced by dry periods. The coincidence with strong wind events resulted in a very strong *I. typographus* outbreak (Skuhravý & Šrot 1988; Pfeffer & Skuhravý 1995). Salvage logging usually exceeds sanitation felling several times. Only during periods of bark beetle outbreaks are these amounts similar, and in exceptional cases sanitation felling exceeds salvage logging. In the period 1964–1991, salvage logging (70 million m^3) was more than five times greater than sanitation felling (13 million m^3).

In most of the Czech territory, a marked (3.5-fold) increase in sanitation felling occurred in 1982–1983. Skuhravý & Šrot (1988) state that such a large increase in damages occurred mainly due to the neglected forest protection and the underestimation of the danger posed by the *I. typographus*. During 1982–1983, a 4.5-fold increase in sanitation felling occurred in the North Moravian State Forests and a 12.9-fold increase in the East Bohemian State Forests. It is probable that in the past the *I. typographus* was not sufficiently recorded at the stated directorates and its numbers were underestimated (Skuhravý & Šrot 1988). A frequent operational misconduct observed even today is purposeful confusion of sanitation felling, which could be subject to sanctions by senior staff or controlling bodies, for salvage logging of abiotic origin. The situation in the East Bohemian State Forests before 1982 directly invites such an explanation. The same registry practices could have also caused marked decreases in sanitation felling reported in 1985 when windfall totalling 7 million m^3 was recorded. It is true, however, that in 1985 the weather during bark beetle swarming was cold (Jančařík & Šrot 1986) and unprocessed wood from windstorms was given preventative treatment in early summer (Skuhravý & Šrot 1988). A similar trend was also recorded in Switzerland, where damage to forest stands by Cyclone Lothar in 1999 led to a decrease in sanitation felling in 2000 (Stadelmann et al. 2014).

Especially during the 1980s, windfall events caused an increase in *I. typographus* abundance and onset of its outbreak. Trees uprooted by wind are considered to be one of the important triggers for large bark beetle outbreaks (Økland & Berryman 2004). Higher reproductive success on windfall (Komonen et al. 2011) enables population density to exceed the threshold level K_3 necessary for colonising standing trees (Berryman 1974; Berryman & Kindlmann 2008; Kausrud et al. 2012). In addition to windfalls as a material without a defence reaction or with a minimal defence reaction, increases in *I. typographus* abundance are also facilitated by the presence of standing spruces that have withstood destructive winds. The root hairs of such spruces have been damaged due to sway motions of trees caused by wind gusts, and such trees are then susceptible to infestation (Skuhravý 2002) in that they are sought by bark beetles even at long distances from windfalls (Jakuš et al. 2003).

In the monitored period the growth in the volume of bark beetles was observed with a delay of 1–3 years. A shift of 1 year was recorded for the East Bohemian State Forests, 1–2 years for the South Moravian State Forests, 2 years for the South Bohemian State Forests, and 2–3 years for the West Bohemian State Forests. The length of the delay was certainly affected by a number of factors that are difficult to describe as a whole. The most important factor was probably elevation, which correlated with air temperature and the number of *I. typographus* generations. The onset of gradation was delayed at mountain locations. Within the Czech lands, this was particularly the case in the Šumava region stretching into the West Bohemian and South Bohemian state forests, where longer delays were observed, as well as in such areas as the Beskids (North Moravian State Forests). However, no significant cross-correlations were found for this region even though sanitation felling in 1983 was preceded by a period (from 1980) with more windfalls (Fig. 1). The onset of *I. typographus* gradation was also affected by the periods of wind disturbances.

The largest correlation coefficient (r = 0.79) was found for a zero delay in the South Moravian State Forests and only this "shift" in the volume of sanitation felling after salvage logging was significant at a nationwide level. The zero delay between wind disturbance and the onset of a bark beetle outbreak may have had several causes. In the case of the South Moravian State Forests, the high correlation between salvage logging and sanitation felling in the same year was caused by this area's warmer and drier climate (cf. Tolasz et al. 2007). Temperature has a crucial influence on the number of bark beetle generations within a given year (Annila 1969; Wermelinger & Seifert 1999; Hlásny et al. 2011). Drought stress also increases the susceptibility of spruce trees to bark beetle infestation (Netherer et al. 2015) in such a way that a lower population density is sufficient to exceed the K_3 threshold level. The effect of drought on *I. typographus* population dynamics deserves a separate analysis, but the comprehensive data on drought incidence are not available for the Czech lands yet. Diligent efforts are being made, however, to validate such data.

Infestation of standing trees in the first vegetation season following wind disturbance also occurs if windfalls are removed before spring bark beetle swarming (Schroeder & Lindelöw 2002). Accelerated clearing of windfalls is common practice in economic forests (cf. Forster 1998), although particularly in dry regions this can lead to the spread of infestation to surrounding standing trees over a considerably large surrounding area and the problems related with processing calamities. From the perspective of effective forest protection management, it is thus appropriate to recommend that windfall be processed after *I. typographus* swarming. Windfallen trees can be used as trap trees to reduce the risk of infestation to surrounding standing trees. When deciding to postpone the processing of either the whole windfall or its certain portion, it is necessary to take the available processing capacity into consideration and to adjust the amount of windfallen wood left on site accordingly so as to prevent the complete bark beetle development in the colonied trunks. From a spatial standpoint, it is beneficial to select easily accessible parts of the wind-fallen area for delayed processing. Especially in the case of large-scale wind disturbances, not all windfall is typically processed in a timely manner. During the monitored period, this was the case especially in the 1980s, and in particular during 1985, when after 30 June 5 million m^3 of wood remained unprocessed in the forest (Skuhravý & Šrot 1988). Such circumstances could have influenced the length of the delay between salvage logging and sanitation felling. Unfortunately, records on unprocessed material are not available from the 1980s as no such item was included in the L116 report. If timely clearing of all windfalls is not possible, it is necessary to develop a plan for processing calamities with regard to the risk that a bark beetle calamity occurs and to apply a single procedure for an area of at least 1–2 km^2 (Forster 1998).

Delays in colonising standing trees are also affected by windfall extent. The switch to standing trees is much faster for small windfalls, while large windfalls may be colonised by *I. typographus* repeatedly. The speed at which standing trees are colonised after wind disturbances depends also on how long windfall remains attractive for bark beetles in a given area (another aspect of the effect of elevation and temperature). Data on the attractiveness period of windfall in various parts of this pest's extended area vary. Under Central European conditions, colonisation of windfall can be expected in the very first vegetation season, as shown for example by Grodzki et al. (2006a, b and 2010) although this infestation may involve the second beetle generation (cf. Modlinger et al. 2009). By contrast, in southern Sweden windfall was infested only in the second vegetation season (Komonen et al. 2011). Kula & Ząbecki (2006) observed colonisation of windfall during two vegetation seasons in the Silesian and Polish Beskids. The attractiveness of windfall for *I. typographus* depends especially on the extent to which the roots maintain contact with the soil (Jakuš 1998a, b). From this point of view, the colonisation is possible under favourable conditions also in subsequent vegetation seasons. Louis et al. (2014) recorded neither significant differences in fecundity, progeny body mass nor any qualitative changes in phloem on trees artificially uprooted 17 months earlier. On the other hand, accelerated desiccation and loss of the phloem's nutritional quality can be expected if there is a greater proportion of snapped trees. A snapped tree indicates a trunk with shattered basal section or crown usually disconnected from the root system (Kula & Ząbecki 2005). Snapped trees are first to be colonised by bark beetles. With extensive windfalls and low *I. typographus* population densities, however, snapped trees do not necessarily have to be colonised. In exposed windfall areas, snapped trees desiccate more rapidly and hence, do not necessarily present a risk of another bark beetle generation developing (Forster 1998).

In addition to the expected increased damages caused by *I. typographus* after previous windfalls, the analysis of the historical data using cross-correlation yielded another notable result: an inverse dependence, i.e. increased damages caused by wind after bark beetle outbreak. A 1-year shift was recorded in the East Bohemia and the South Moravia; 2-, 3- and 4-year shifts were detected in three of the regions; and a 5-year shift was evident only in the East Bohemia. This surprising trend was demonstrated also at a nationwide level (significant shifts by 1, 2, and 3 years).

It may be assumed that sanitation felling, which exposes previously protected stand walls to destructive winds, also leads to the occurrence of windfalls. In this case, the shift is a function of the period of wind events, so its length is random. The influence of the stand edge on forest stand stability has been known for a long time (Vicena et al. 1979; Schindler et al. 2012), and the creation of a functional stand edge requires a number of years. Due to competition, spruce trees growing inside connected stands have less developed root systems and smaller crowns (i.e. high centres of mass). If due to a disturbance such trees appear on the stand's edge, they become much more vulnerable. In addition, the newly formed stand edge has not created a cover and its entire crown area is exposed to wind (Dupont & Brunet 2008). The most important stand characteristics influencing its susceptibility to strong wind include species composition and stand height, but also certain variables characterising the amount of previously harvested wood as a part of timber management (Klopčič et al. 2009; Albrecht et al. 2012) or during interventions against pests (Jalkanen & Mattila 2000). It is apparent that previous forestry interventions play an important role in forest stand stability against wind. In the East Bohemia, only a single bark beetle outbreak in 1984 resulted in increased salvage logging observable for the entire remainder of the monitored period. According to Hanewinkel et al. (2008), the periodicity of damages by wind and snow at an interval of 1–2 years indicates a destabilised forest stand.

In the case of two regional forest state directorates, significant cross-correlations were recorded only for the delayed wind damages after sanitation felling. These cases consisted of *I. typographus* outbreaks without the triggering role of windfall. In the North Bohemian State Forests, the greatest impact certainly stemmed from pollutants, as this region was among the most pollution-affected regions in Europe (Fiala et al. 2002). Drought and neglected forest protection could be regarded as the most significant factors in the Central Bohemian State Forests.

Statistically significant cross-correlations for both types of relationships (sanitation felling after wind damage and salvage logging after bark beetle outbreaks) were determined in three regions. The curves for salvage logging and sanitation felling with no mutual shift are very similar in the South and West Bohemia. A relatively weak bark beetle outbreak occurred at the start of the monitored period, and was followed by an increase in wind damages two years after its peak. In the 1970s, on the other hand, wind damage was followed by bark beetle infestation. A strong large-scale bark beetle outbreak began in the 1980s, during which wind had also an increased impact and, due to the presence of windfall, an acceleration in *I. typographus* outbreak also occurred. After the stabilisation of the bark beetle outbreak in the early 1990s, extensive wind damages occurred again. These regions suffered from most of the damages by wind and by bark beetles during the monitored period. The South and West Bohemia are cold regions with high elevations, substantial proportions of spruce, and total precipitation relatively optimal for spruce (Table 1). Tree dimensions and elevation are factors that substantially affect damages to stands by the wind-bark beetle system (Mezei et al. 2014).

At the onset of a gradation following a wind disturbance, windfall clearings are further extended due to the performance of sanitation felling. This increases the length of the newly created stand edge, which is evened out and destabilized by the wind (Vicena et al. 1979; Schindler et al. 2012), thereby creating further windfall suitable for bark beetle reproduction. In addition to decreased static stability, however, trees in the newly created stand edges suffer from the insolation stress. These locations then become attractive to bark beetles (Forster 1998; Schroeder & Lindelöw 2002). Removal of an affected stand (whether due to wind or bark beetle disturbance) always results in a clearing with an unstable stand edge.

Renewing the practice of protecting forest stands from destructive winds is a long-term process, usually requiring more than ten years (e.g. Vicena et al. 1979). Although predictions of future climate development are not uniform among current scientific studies, scientists usually agree in expecting increased frequency of extreme phenomena such as destructive winds (Lindner et al. 2010) and droughts (Hlásny et al. 2014). Disturbances to forest stands will therefore continue to be regarded as an important factor driving the occurrence of bark beetle outbreaks in the near future.

5. Conclusion

The presented overview of damages caused by wind and by European spruce bark beetle over the period 1964–1991 provides a comprehensive time series at a level of the former regional divisions of Czech lands. In the given period, salvage logging (70 million m^3) was more than five times greater than the volume of sanitation felling (13 million m^3). Damage intensity gradually increased during the monitored period. Cross-correlation between the time series demonstrated an increase in *I. typographus* abundance and the onset of its gradation as a consequence of windfall events. The increase in the volume of infested wood was observed with 1- to 3-year-long delay. The pressure on forest management to accelerate the processing of windfall before spring bark beetle swarming is a frequent cause of high sanitation felling in the same year. It is possible that in the Czech lands such circumstances yielded the resulting zero delay in calculating the cross-correlation.

The cross-correlation between the time series also demonstrated a significant shift in wind damage after sanitation felling with a delay of 1–5 years. It may be assumed that sanitation felling results in the exposure of previously protected stand edges to strong winds, which in turn leads to windfall events in these locations. In such cases, the length of the shift is a function of the period of wind events, i.e. the stochastic component. Disturbance of forest stand static stability may be considered as one of the main harmful consequences of bark beetle outbreaks for the near future

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