Lesn. Cas. For. J. 62 (2016) 15–22

ORIGINAL PAPER

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

Elevated bark temperature in unremoved stumps after disturbances facilitates multi-voltinism in *Ips typographus* population in a mountainous forest

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Abstract

The number of *Ips typographus* generations developed in a year might be indicative of its population size and of risk to Norway spruce forests. Warm weather and unremoved fallen trees after natural disturbances are thought of as key factors initiating large population increase. We studied *I. typographus* development in a spruce forest of the Tatra National Park, which was heavily affected by large-scale disturbances in the last decade. Repeated windthrows and consequent bark beetle outbreaks have damaged almost 20,000 hectares of mature Norway spruce forests, what is a half of the National Park forest area. Current *I. typographus* population size and its response to the environment and to forestry defense measures attract attention of all stakeholders involved in natural resource management, including public. In this paper we analyse the potential *I. typographus* population size in two consecutive years 2014 and 2015, which represented a climatologically normal year and an extremely hot year, respectively. We used bark temperature and phenology models to estimate the number of generations developed in each year. In 2014, the average bark temperature of standing living trees at study sites was 14.5 °C, in 2015 it increased to 15.7 °C. The bark temperature of fallen logs was 17.7 °C in 2014, and 19.5 °C in 2015. The bark temperature of standing living trees allowed to develop one and two generations in 2014 and 2015, respectively. The elevated bark temperature of fallen logs allowed to develop two generations in 2014 and three generations in 2015. The good match between the predicted and observed timing of each generation emergence as well as the large increase in the number of catches in pheromone traps in 2015 indicated a dramatic increase of the *I. typographus* population in the extremely warm year, especially at the unmanaged windthrown site.

Key words: Norway spruce stands; European bark beetle, bark temperature; PHENIPS, disturbances

Editor: Tomáš Hlásny

Introduction

The European spruce bark beetle *Ips typographus* is natural component of Norway spruce forest in Europe. It plays an important role in natural forest cycle by decomposing wood, sustaining nutrient availability and production capacity in long term (Christiansen et al. 1987). On the other hand *I. typographus* is also one of the most important forest pests in Europe (Wermelinger 2004; Blackwell et al. 2013; Schelhaas et al. 2003). *I. typographus* prefers to reproduce in breeding material with non-existing or weak defence such as wind-felled or otherwise damaged trees (Schroeder & Lindelöw 2002). Blow down of entire stands usually provide an excess supply of nutrition and breeding substrate which is a main trigger of mass bark beetle outbreaks (Wermelinger 2004; Netherer & Nopp-Mayer 2005; Faccoli 2009). Mass attack is the strategy of *I. typographus* to overcome the defence mechanism of the trees (Christiansen et al. 1987; Raffa et al. 2008). Large population is able to kill also apparently healthy trees in large numbers. Large-scale windthrows with surplus of food, breeding material and limited defence allow easier colonisation with less dense population. Lower intraspecific competition and consequently stronger and bigger progeny in broken trees stimulates a mass attack on the surrounding healthy trees. To prevent such population increase, removal of wind-felled spruce trees after storm disturbances has been the long practice whenever possible.

Bark beetles are ectothermic organisms, their body temperature depends on the surrounding environmental conditions. Ambient temperature practically controls course of development stages (egg, larvae, pupae, imago), as well as the spring swarming, and population size (Wermelinger & Seifert 1998). Under warmer conditions *I. typographus* is a multivoltin organism. Two generation could emerged in central, or even three, in southern Europe, while in Scandinavia, and mountainous regions, one generation is the most common (Lange at al. 2006). Understanding of *I. typographus* phenology helps to estimate its population size. Close relation between temperature and insect development is a base of phenological models. Baier et al. (2007) developed PHENIPS, model for monitoring generation development and phenology of *I. typographus*. Number of generations per year is one of the key factors for potential tree attack, ranging from tree-wise up to stand or even region-wise (Netherer & Nopp-Mayr 2005). Large *I. typographus* outbreaks in recent

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decade in central Europe (Wermelinger 2004; Berec et al. 2013) and in Scandinavia (Jonsson 2009) attracted broad attention to this bark beetle by analysing and modelling the impact of climate change, stand predisposition, role of natural enemies in population dynamic, winter mortality, population size and other factors controlling the *I. typographus* populations (Hlásny & Turčáni 2009). Warm and dry seasons become more frequent and long elsewhere in mountainous regions due to changing climate and very likely stimulate bark beetle population growth.

Forest in Tatra National Park is naturally dominated by Norway spruce with frequent large-scale wind distubances. During last 10 years the region has been strongly affected by several extraordinary weather events. Windstorm in 2004 flattened 12 000 hectares of spruce forest (30% of total forest cover in National Park) mostly in lower altitudes. Windstorm in 2014 damaged roughly 2500 ha, mostly stands in higher elevations, close to the timber line. According to long-term meteorological observation in the Tatra Mts. region summer temperature is increasing. Eight out of ten last years were warmer than long-term average. The 2015 summer was the warmest in the last 100 years.

Bark beetle outbreaks have always occurred in the Tatra Mts forest, esp. when wind damage coincided with warm and dry seasons. To prevent mass outbreaks sanitary cutting has been used as the standard forest management method for decades in the Tatra National Park. Recently this prevention measure was restricted and allowed only outside the core zone of the National Park. Prognosis for possible forest damage by bark beetle after large-scale disturbances were controversial, spreading from no damage to the total destruction. In reality, since 2007 bark beetle killed more than 7 000 ha of mature spruce forest. Fragmented spruce stands became more sensitive especially to wind disturbances and almost every year several hundreds of ha of mature forest have been fallen. Due to nature conservation rules and partly remoteness of affected sites large areas were left without any controlling measures against bark beetle outbreaks.

Our aim was to describe bionomy of *I. typographus* under normal and extreme weather in the Tatra Mts. The objective was also to estimate potential *I. typographus* population according to contrast post-disturbance management (removed *vs*. unremoved fallen trees). In this paper we interpret number of generation as an indicator of population size and thus potential risk of bark beetle attack on surrounding healthy forest. Specific aim was to estimate phenological development according to directly measured bark temperate and compare it with the model PHENIPS (Baier et al. 2007).

2. Material and methods

2.1. Study site

We studied the *I. typographus* population dynamic on two localities in Tatra National Park, which are part of the international long-term ecological monitoring and research projects (ILTER, EXPEER). The study sites Vyšné Hágy (VH) and Tatranská Lomnica (TL) are located on the edge of the 2004 windthrow and at present are affected by bark beetle outbreaks. Before the disturbances mature seminatural and natural Norway spruce stands dominated on study sites. The sites are fully equipped for continuous measurement of environmental parameters (Fleischer 2008). Terrain on both of the localities is relatively flat, well exposed to incoming solar radiation, with no obstacles from peaks. On the VH site few tall trees remained. Description of the study sites is in Table 1.

We compared *I. typographus* development under contrast weather conditions in 2014 and 2015. The 2014 represents normal temperature and high precipitation, while the 2015 was extremely warm and dry. According to the Slovak Hydrometeorological Institute the 2015 summer in Tatranská Lomnica (830 m a.s.l.) was the warmest since 1898. Average air temperature during growing season (April 1st to August 31st) in 2015 was 15.4 °C what was 1.9 °C above the 1930–1960 average (13.5 °C). In 2014, the average air temperature (13.7 °C) was nearly equal to the long-term normal. Precipitation in 2014 was 572 mm which was 38% above and in 2015 the precipitation sum was 40% below normal (415 mm) and was the second driest in history.

2.2. Phenology of *Ips typographus*

Phenology models describe the beetle´s development stages (egg, larvae, pupae, adult) according to the ambient temperature. We have used threshold values and sum of temperature (so called degree-days, DD) as suggested by Wermelinger & Seifert (1998), shown in Table 2. Phenological development allows to estimate potential number of generations what is crucial for estimation of *I. typographus* population size a thus potential risk for forest. By calculation of DD required for individual stage development we could estimate time of spring swarming, the onset of infestation, the re-emergence of parental beetles, and the number and emergence time of the regular and sister brood as proposed in the PHENIPS model by Baier et al. (2007). Detailed phenological development is needed for estimation of development completeness in late autumn. Since only young adults can successfully survive winter hibernation late autumn developmental stage is crucial for next year population size (Facoli 2002; Netherer 2003). PHENIPS allows to estimate maximum number of

Table 1. Location and characteristic of study sites.

Site name	Alt [m a.s.l.]	WGS E, N	Slope [%]	Orientation	Specific description
Vyšné Hágy – VH-	1200	20° 06´ 30´´ 49° 07´ 30´´	0 – 5	S	Managed zone of NP, in May 2014 50 ha windthrow in vicinity, partly hit the site, fallen wood removed in summer of 2015
Tatranská Lomnica – TL-	1150	20° 14´ 50´´ 49° 10´ 45´´	10 – 15	S	Border between managed and unmanaged zone of NP, continuous IT outbreaks in the site vicinity

generations on regional scale as well as actual state of the bark beetle development on a specific tree level.

Table 2. The lower threshold value and the number of degree-days to complete the development of each developmental stage of *I. typographus* (Wermelinger & Seifert 1998).

Phase	Treshold value °C	ET sum (DD) °C
Egg	10,6	51,8
Larvae	8,2	204,2
Pupae	9,9	57,2
Adult	3,2	245

For sister generation development we add regeneration period defined by 8.3 °C as the threshold and 278 DD as effective temperature sum proposed by Wermelineger & Seifert (1998).

While the phenology model is an estimation of *I. typographus* bionomy, catches in pheromone traps mirror real population dynamic (onset of spring swarming, development of the filial generation and the establishment of sister broods). Every year we have installed 25 traps in the vicinity of each study site. Catches in the traps were sampled every 10 days by local foresters.

2.3. Climate data and bark temperature

Phloem (bark) temperature depends on direct solar radiation and ambient air temperature. Average 60 min radiation and temperature were recorded using a sensor EMS11 (EMS Brno, CZ). Bark temperature was measured with a resistance thermometer Pt1000 (10/1 mm) and recorded by MicroLog SP3 (EMS Brno, CZ) as 60 min average. We drilled 1 mm diameter holes and inserted probes directly into *I. typographus* galleries. We equally sampled both sun exposed and shaded sites of standing live trees as well as fallen logs and for further calculations used average values. The bark temperature was measured in mature trees of representative size for the study sites. For measurement in fallen trees we chose stumps fallen in the previous year (2013 at TL, and 2014 at VH respectively).

Bark temperature is rarely measured in field. Baier et al. (2007) constructed a regression between ambient environmental factors (air temperature and solar radiation) and bark temperature as a part of the PHENIPS model:

$$BT_{avg} = a + b * SR + c * AT_{mean} \qquad [1]$$

Where BT_{avg} is diurnal average bark temperature, SR is the daily sum of the incoming solar radiation (Wh m^{-2}), AT_{mean} is the daily average air temperature (°C).

3. Results

In phenological models bark temperature serves for calculation of thermal sum needed for completion of developmental stages and estimation of number of generations. Beside climate we found tree health status as another prominent factor controlling bark temperature.

3.1. Air temperature and solar radiation

We measured climate parameters from April 1st to mid-September, a period usually favourable for *I. typographus* development, on study sites in two consecutive, but meteorologically contrast years. In 2015 the average air temperature was higher by +0.8 °C than in 2014 (12.1 °C in 2014 and 12.9 °C in 2015 at TL and 11.1 °C and 11.9 °C at VH, respectively). Sum of solar radiation was higher in 2015 on both study sites (1.15 at TL and 1.43 fold at the VH site). Increase of solar radiation at VH was caused by a windthrow in May 2014 and consequent dieback of individual shading trees at the study site. Diurnal air temperature and solar radiation sum (kWh) for TL and VH sites are shown in Fig. 1.

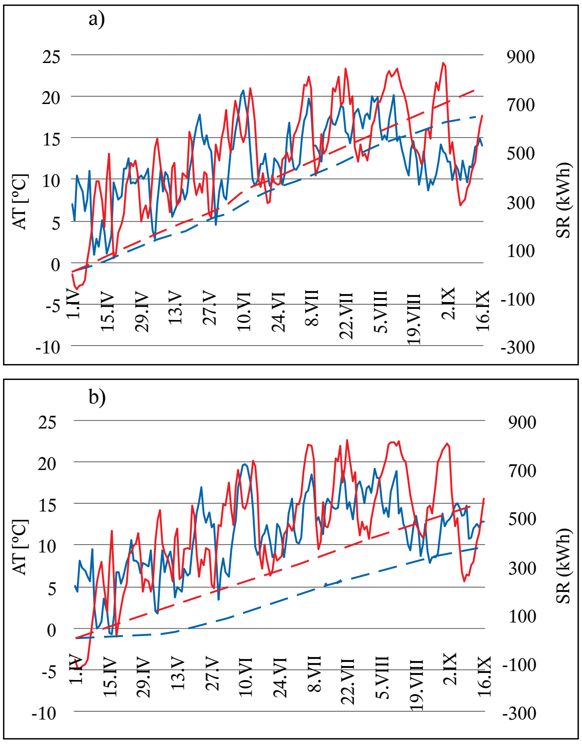


Fig. 1. Average diurnal air temperature (°C) and cumulative solar radiation sum (kWh) in 2014 (dark) and 2015 (light) at (a) Tatranská Lomnica and (b) Vyšné Hágy study sites.

3.2. Bark temperature

Bark temperature was directly measured in phloem of the fallen trees in 2014 at TL (n = 3) and both live (n = 3) and fallen trees (n = 5) at VH in 2015. Missing data for comparison between the years and tree status (live vs fallen) were derived from regression with the air temperature and solar radiation, as proposed by the PHENIPS model. We derived the parameters for equation [1] by the use of multiple linear regression with ordinary least square estimation (Statistica v.7, StatSoft, Inc.) on directly measured bark temperature on both live and fallen trees. In Table 3 we present regression parameters (a, b, c), regression coefficients (R^2) and mean square errors (MSE). For comparison we show also parameters proposed by Baier et al. (2007) and PHENIPS performance with standing live trees at our study sites.

Table 3. Regression parameters for estimation of bark temperature using equation [1].

Model/parameter	a	b	c	R2	MSE	Notes
PHENIPS	−0,173	0,0008518	1,054	95,9	2,41	Baier et al. (2007)
Standing live trees	−0,567	0,0002550	1,031	97,2	0,82	
Fallen trees	−1,811	0,00151	1,079	91,9	1,51	

In Table 4 we show average bark temperature directly measured and modelled at the study sites in 2014 and 2015. Measured data are labelled with an asterix.

Table 4. Bark temperature in °C (L – live, F – fallen trees) at the VH and TL site in 2014 and 2015, * indicates directly measured data.

	TL		VH	
	L	F	L	F
2014	13,9	18,6*	15,0	16,8
2015	15,6	20,7	15,8*	18,3*

Seasonal course of average diurnal bark temperature in live and fallen trees at study sites in 2014 and 2015 is shown in Fig. 2a and 2b.

In 60% of all diurnal averages, the fallen logs were warmer by 2 ÷ 4 °C than standing living trees. The maximum difference in the daily average was 8.7 °C. The maximum hourly values occasionally exceeded 40 °C in logs and 25 °C in living trees.

3.3. Phenology and number of generations

Spring swarming was estimated from the maximum diurnal air temperature. According to Zumr (1982), and confirmed by previous field observations (Tatra National Park forestry evidence, internal data), we used threshold value of 7 °C and 145 °C sum of effective temperature for estimation of first flights. Real flights started after completeness of required sum, in sunny days when daily temperature in three consecutive days exceeded 16 °C.

Differences in bark temperatures between the observed years as well as differences between forest statuses (standing live versus fallen trees) caused remarkably different phenological development. To demonstrate the influence of exceptionally warm weather in 2015 we compare *I. typographus* phenological development in living trees with the 2014 development on both the study sites (Fig. 3). To illustrate the influence of tree status (live versus fallen) we compared phenological development in live and fallen trees in 2014 at TL and in 2015 at VH (Fig. 4).

At the TL site bark temperature in 2014 (Fig. 3a) allowed to emerge one generation and allowed one sister generation to develop up to immature adult stage. In 2015 warmer environment allowed to emerge one parental and one sister generation. First filial generation also fully developed (Fig. 3b), but did not emerge due to the daylight length limit August. Daylight below 14.5 h (Doležal & Sehnal 2007) eliminates *I. typograhus* emergence. At the study sites a critical day is on August 20th.

At the VH site in 2014 also one generation emerged, but sister generation developed only up to the stage of early immature adult (Fig. 3c). In 2015 sister generation fully developed and probably successfully overwintered. The first filial generation developed up to the stage of pupae and chance for successful overwintering was questionable (Fig. 3d).

Contrary to live trees in 2014 at TL bark temperature in fallen trees allowed to emerge also the sister generation. Filial generation reached the stage of immature adult with high chance for successful overwintering. Second sister generation reached the stage of pupae (Fig. 4a). In 2015 under extremely warm weather bark temperature in fallen trees at the VH site allowed 3 generation development. Also 1st and 2nd sister generation fully developed, as well as 1st sister filial generation (Fig. 4b).

3.4. Catches in pheromone traps

Average numbers of *I. typographus* catches by pheromone traps in the vicinity of the study sites in 2014 and 2015 is shown in Fig.5. While in 2014, the catches on the study sites were rather similar, in 2015 the numbers of the insect increased, esp. on TL site, almost two-fold. Remarkable was the increase of late summer catches on both localities.

4. Discussion

Enhanced summer temperature is the driving forces for the spread of bark beetles into higher altitudes and latitudes (Jonsson et al. 2011). Recent warm summers and repeated windthrows stimulated large *I. typographus* populations and vast tree dieback in mountainous Norway spruce forest across the entire Slovakia (Kunca et al. 2015; Vakula et al.

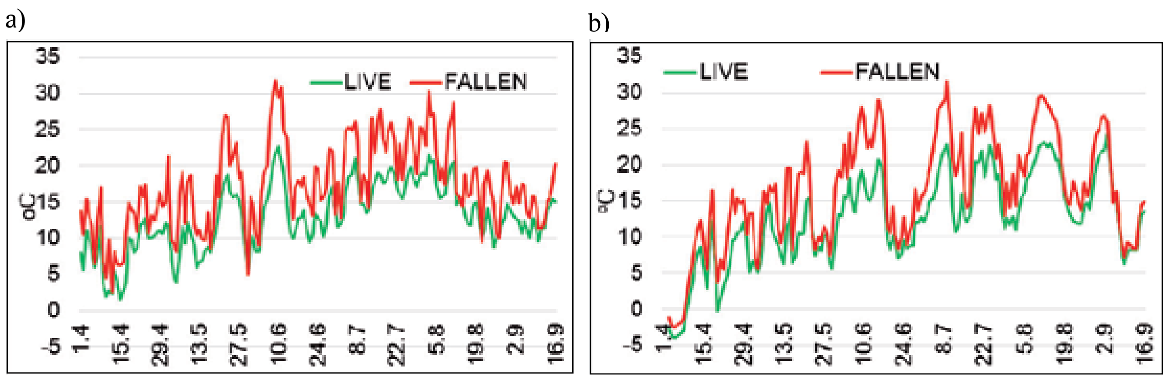
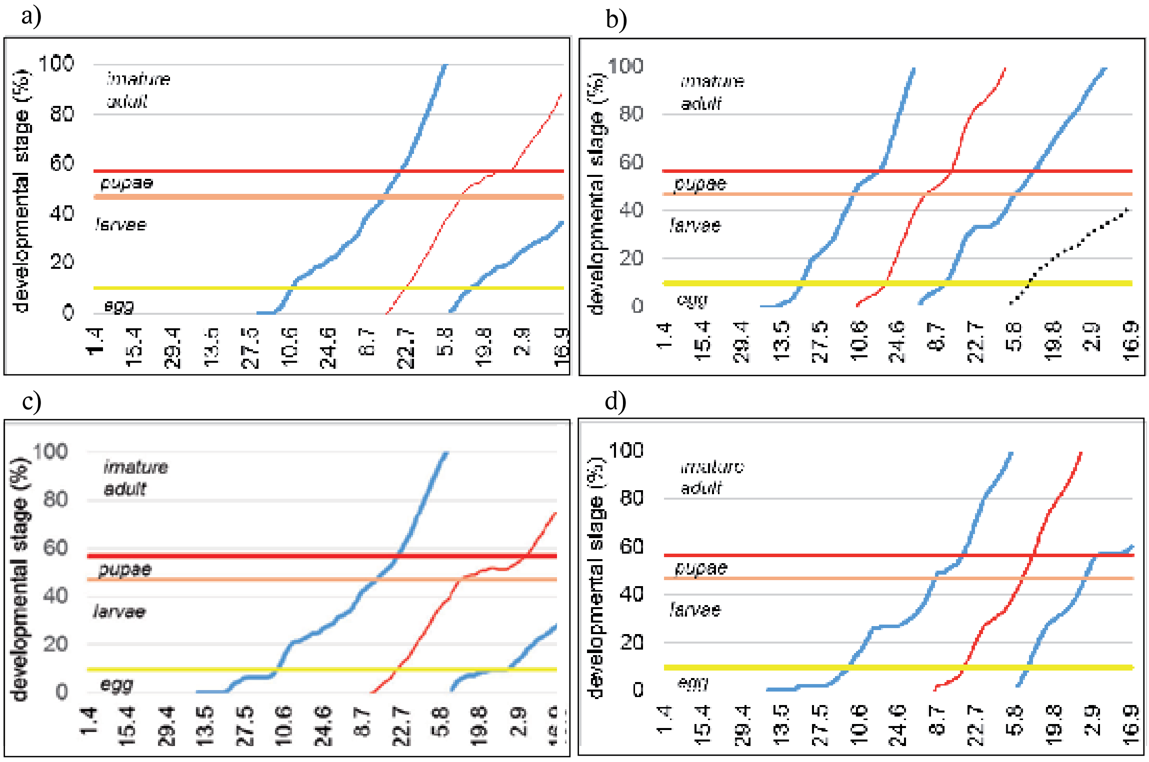
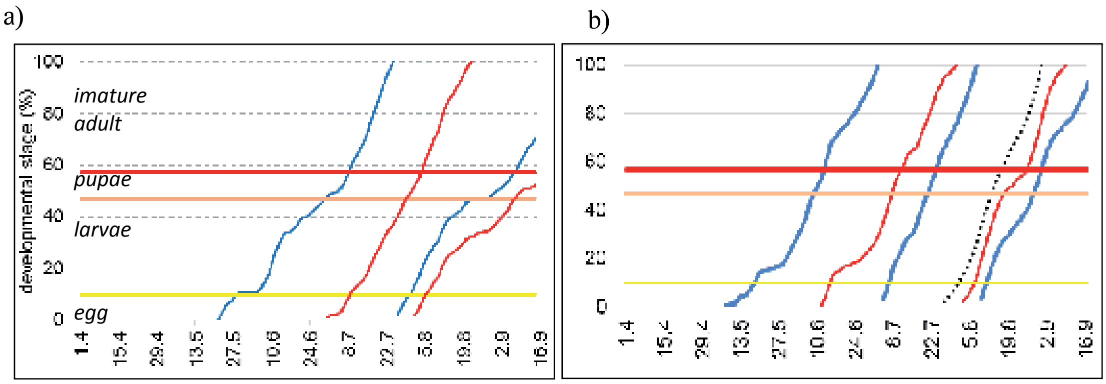


Fig. 2. Average diurnal bark temperature (°C) in live and fallen trees (a) TL 2014, (b) VH 2015.



Legend: blue line: main generations – parental, 1st and 2nd filial generation, red dotted ine: 1st sister filial.

Fig. 3. Comparison in phenology and number of *I. typographus* generations (a) TL 2014, (b) TL 2015, (c) VH 2014, (d) VH 2015 on live trees.



Legend: blue line: main parental, 1st and 2nd filial generation, red line: 1st and 2nd sister, dotted line: 1st sister filial.

Fig. 4. Potential temporal development and number of generations of *I. typographus* fallen trees, (a) Tatranská Lomnica 2014 (b) Vyšné Hágy 2015.

2015; Bucha & Hlásny 2015). In the Tatra Mts. region the 2014 summer was climatologically normal, while 2015 was extremely warm. The average air temperature in Tatranská Lomnica (830 m a.s.l.) was the highest since the regular observation in 1898 started. Study sites established to analyse *I. typographus* development under different environmental and management conditions were located in higher altitude (1,200 m a.s.l.). Naturally, at this height the air temperature was not so high and also the difference between 2014 and 2015, was not as evident as in lower elevations.

We used bark temperature as a predictor for *I. typographus* development. This method based on Baier et al. (2007) PHENIPS model for estimation of potential numbers of generations and thus impact on surrounding forest has been successfully used in the Alps (Blackwell et al. 2013), Bohemian forests (Berec et al. 2013). The PHENIPS model was built for standing trees inside forest stand, where solar radiation was strongly reduced by canopy. Solitaire trees on our study sites were fully exposed to direct radiation. Under these conditions PHENIPS overestimated bark temperature when compared with directly measured in standing live trees (MSE=2.41). Overestimation was also reported Berec et al. (2013). Applying site specific parameters for live and fallen trees improved estimation of bark temperature (MSE=0.82 for live and 1.51 for fallen trees).

In 2014 under normal weather conditions the univoltine *I. typographus* development happened. Second generation was established, but could reach the stage of larvae only. Elevated air temperature in combination with enhanced solar radiation in 2015 allowed one more *I. typographus* generation (filial) to fully develop at the TL site, or to reach the stage of immature adult at the VH site when compared with the

2014. In the warmer 2015 year also 1st sister generation could fully develop and emerge. In the previous year the sister generation reached immature stage only. Fully developed adult beetles have much higher chance to successfully overwinter than earlier developmental stages. Critical stage is "pupae", below this stage (marked by red line in phenological graphs), the chance to survive winter is very low (Faccoli 2009). The bigger the population size in next spring the more extended damage on forest. Large *I. typographus* infestations due to elevated air temperature were recently reported from the Alps (Stadelmann et al. 2013). The temperature was a driving factor also for the damage of more than 14 mil ha of *Pinus concorta* in Canada (Safranyik et al. 2010).

Bark temperature in fallen trees was higher than in standing live trees by 1.8 – 4.9 °C (span of seasonal averages on all sites and years). Such bark temperature increase caused almost bivoltine development in 2014 (first filial generation reached the stage of mid immature adult and sister generation fully developed). In 2015 two main generation fully developed and 3rd reached 90% of full stage. Warm autumn 2015 very likely allowed complete development before winter. Beside two sister also 1st sister filial generation could fully develop.

Unremoved fallen logs after large-scale disturbance are generally thought of as the key risk factor for infestation of the remaining forest (Wermelinger 2004; Wichman & Ravn, 2001). Schroeder & Lindelöw (2002) reported twice as many trees killed by *I. typographus* in southern Sweden after the 1995 windstorm in unmanaged rather than managed stands. Stadelmann et al. (2013) confirmed the importance of salvage logging for reducing *I. typographus* infestation after the large-scale Lothar wind disturbance in Switzerland.

To prevent *I. typographus* population increase, removal of wind-felled spruce trees after storm disturbances has been the long practice also in the Tatra National Park whenever possible. Forest in central part of the Tatra National Park is naturally dominated by Norway spruce. High frequency of severe wind disturbances (Zielonka et al. 2009) prevent forest to became more structurally diversified. Relatively homogenous spruce stands are prone to bark beetle outbreaks, which regularly occur after wind disturbances. Current enormous bark beetle outbreak started 3 years after the 2004 large-scale windthrow (12 000 ha) and so far have destroyed 7 000 ha of mature spruce stands. Majority of remaining mature stands are located in strictly protected zone of the National Park with no control measures against bark beetle outbreaks. Strongly fragmented stands become more susceptible to biotic and abiotic agents. Climate change scenarios expect more wind disturbances in future. As the area of low forestry management approach increases, future forest status becomes very challenging. In the literature, the potential for bark beetle outbreaks from unmanaged windthrow is explained by luxurious food and breeding possibilities in defence-limited and less competitive intraspecific environment (Wermelinger 2004).

Estimated number of *I. typographus* generations is theoretical maximum under existing weather conditions. Despite key role of generation numbers for population size, in reality population might be influenced by numerous external and internal factors and differ significantly from modelling. Comparison of predicted bark beetle emergency dates with catches in pheromone traps confirmed good performance of prediction and usefulness of predicted data for resources managers. Although, the accuracy estimation is difficult due to 10-day collection of catches in pheromone traps and differences among some generation emergence days were sometimes only few days as shown on Fig. 4 and 5.

We found bark temperature on fallen trees to play crucial role in population development. Only little can be found in the literature about fallen tree's bark temperature and population size. One of the reason could be the general opinion about fast drying-out of fallen logs. Dry phloem is no more suitable for establishment and development of new insect populations. Observation from the 2004 unmanaged windthrow confirmed the existence of living uprooted trees even four years after the event. Stadelman et al. (2013) found three years after disturbance as still suitable time for *I. typographus* colonisation in higher altitudes. Higher temperature in fallen logs should be explained by a missing transpiration flux. Also, the reduction of ground level wind speed by surrounding structures might increase the temperature.

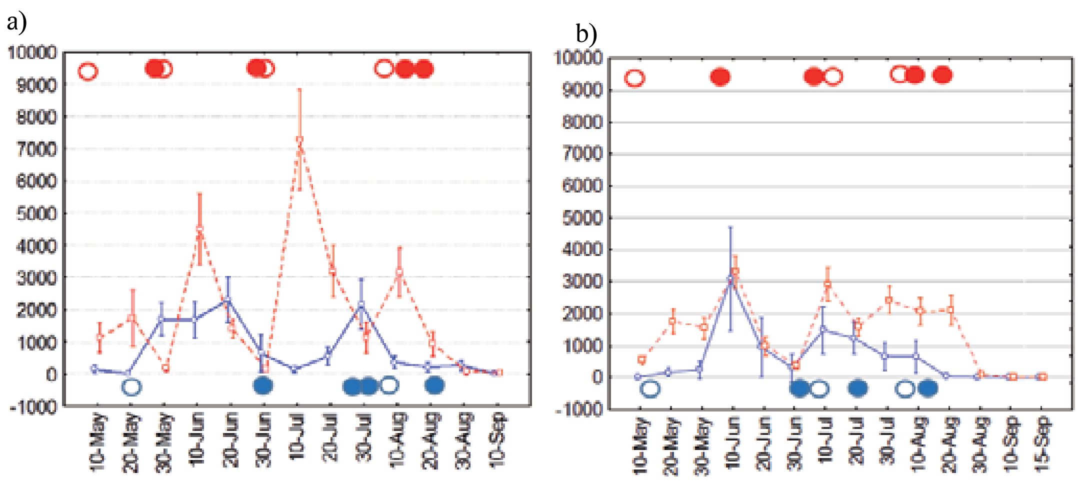


Fig. 5. Number of *I. typographus* individuals in pheromone traps (means and standard errors) in 2014 (blue) and 2015 (red) at (a) Tatranská Lomnica, (b) Vyšné Hágy. Dots represent calculated date of individual generation emergence presented in Fig. 3 and 4: blue circle-emergence from live trees 2014, blue dot-emergence from fallen trees 2014, red circle-emergence from live trees 2015, and red dot-emergence from fallen trees 2015.

5. Conclusion

We analysed the development of *I. typographus* in Norway spruce forest in Tatra National Park affected by strong disturbances, weather extremes and different post-disturbance forest management in recent years. We chose two years representing normal (2014) and elevated air temperature (2015). On two study localities we estimated *I. typographus* development in standing and fallen trees, representing contrast management methods (fallen trees removed vs. left on site). We used effective heat sum to estimate the *I. typographus* phenology, potential number of generations and thus possible risk for the remaining mountainous spruce forest. Heat sums were derived from directly measured and modelled bark temperature. Elevated air temperature increased also temperature in phloem of standing live trees and allowed one more generation to develop. Bark temperature in one year old fallen logs was warmer than bark in standing trees and allowed two generations to develop in climatologically normal and even three main generations in extremely warm year. Catches in pheromone traps confirmed realistic estimation of *I. typographus* generation numbers and their emergence time by phenological models. Accordingly we can conclude that majority of the *I. typographus* population in study sites developed in fallen trees.

The results showed the importance of increasing air temperature on *I. typographus* population. Current extremely high summer temperatures are likely to persist in the future, and bivoltine bark beetle populations might affect adversely also mountainous spruce forests. Our finding on elevated temperature in fallen trees stimulating at least one more generation could explain reasons for enormous bark beetle outbreak 2 – 3 years after the 2004 large-scale windthrow and also might influence further decisions about post-disturbance management in protected area. The results hopefully might attract more attention to study very complex bark beetle population dynamic after natural disturbances and under changing environmental conditions.

Acknowledgement

This work was supported by the Slovak Grant Agency APVV, No. 0480-12 and ITMS 26220220087 funded by the Operational Program for Research and Development and co-financed by European Fund for Regional Development. The authors are grateful to the State Forest of Tatra National Park for support and pheromone traps data and especially to L. Berec and T. Hlásny for valuable comments and substantial improvement of the manuscript.

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