Folia Forestalia Polonica, Series A – Forestry, 2019, Vol. 61 (3), 174–181

ORIGINAL ARTICLE

DOI: 10.2478/ffp-2019-0017

The European spruce bark beetle *Ips typographus* (L.) in wind-damaged stands of the eastern part of the Tatra National Park – the population dynamics pattern remains constant

Wojciech Grodzki[1] ✉, *Wojciech Gąsienica Fronek*[2]

[1] Forest Research Institute, Department of Mountain Forests, ul. Fredry 39, 30-605 Kraków, Poland, e-mail: W.Grodzki@ibles.waw.pl, ORCID 0000-0003-0623-752X

[2] Tatra National Park, Kuźnice 1, 34-500 Zakopane, Poland

Abstract

In March 2017, in the eastern part of the Tatra National Park in Poland, large windthrowns affected the passively and actively protected Norway spruce *Picea abies* stands. In early 2018, a set of 12 small research plots (20 trees on each plot) was established in the Norway spruce stands next to the windblown area – 6 in the stands under active nature protection (broken and fallen trees processed in 2017), and 6 in the stands under passive nature protection (trees left on the ground). Living trees on the plots were regularly checked during the growing season in order to identify and register the spruces infested by *Ips typographus,* which were dissected in 2 or 4 half-meter sections. 155 spruces (64%) infested by *I. typographus* were recorded on all 12 plots: 118 out of 120 (98%) in passive and 37 out of 120 trees (31%) in active protection. Mean infestation density calculated on 128 samples from 47 trees was higher under passive than under active protection (1.23 and 0.92 mating chamber per 1 dm^2, respectively). Among 1709 gallery systems, those with 2 maternal galleries prevailed (63.0%); the mean share of females was higher in passive than in active protection zone (63.1 and 59.6% respectively). The mean number of progeny per one female was higher in active than in passive protection zone (20.23 and 19.12 respectively). *I. typographus* attack on standing trees had lower intensity in the stands previously subjected to the processing and removal of fallen and broken trees, which indicates positive effect of implemented active protection procedures. The parameters describing *I. typographus* population on attacked trees, as well as low activity of natural enemies, demonstrate its reproduction potential and resulting high risk of a new outbreak, according to the pattern known earlier from the other areas in Poland and Europe.

Key words

Picea abies, mountain forests, insect outbreak, nature conservation

Received 17 May 2019 / Accepted 25 July 2019

Introduction

At the end of 2013, in the western part of the Tatra National Park in Poland (mainly in the area surrounding the Kościeliska Valley), large windthrowns affected the Norway spruce *Picea abies* (L.) H. Karst. stands located in both active and passive protection zone. In 2014–2017, the survey of the spruce bark beetle *Ips typographus* (L.) (Col., Curculionidae, Scolytinae) occurrence was conducted on and next to the area of such damaged stands (Grodzki and Gąsienica Fronek 2017a, b, 2018). The results confirmed the findings already known from several parts of Europe, that starting from the second growing season after the damage, the fast increase in the bark beetle population density occurs, which signify the beginning of its outbreak (Lindelöw and Schroeder 1998; Göthlin et al. 2000; Meier et al. 2003; Grodzki et al. 2007). The later abandonment of classic bark beetle control measures in the attacked stands under active protection led to the rapid acceleration of the mortality of spruce trees, that totally suppressed the positive effect achieved earlier by the removal of broken and fallen trees (Grodzki and Gąsienica Fronek 2018).

In March 2017, on the area of the Tatra NP, the recurring damage (about 3.2 thous. m^3) caused by foehn wind affected the Norway spruce stands located in its central and eastern part, mainly in lower forest zone. This phenomenon opened the opportunity for a new survey that could serve for the validation of the pattern that depict the early stage of *I. typographus* outbreak, described earlier in the Kościeliska Valley, and to estimate the effect of the applied forest protection approach on the population dynamics of this insect species.

The main aim of the study was to assess the effect of applied protection strategy (broken and fallen trees removed or left in the forest) on the population of *I. typographus*, and its resulting pressure on the trees that survived the wind disaster. The results could serve in the planning of necessary control measures in the damaged stands under active protection, facing the expected bark beetle outbreak.

Material and methods

The study was done in the Kośne Hamry forest range in the eastern part of the Tatra NP, in selected stands damaged by the wind in 2017. In early 2018, a set of 12 small research plots was established in the recently opened edges of the 80–100 years old Norway spruce stands next to the windblown area, from which 6 were located in the stands under active nature protection, where broken and fallen trees were processed in 2017, and next 6 in the stands under passive nature protection, where those trees were left on the ground. The selection of plot location was done based on the real protection procedure applied, regardless their location in the formally defined nature protection zones of the Park. The whole set of plots was included in the rectangle area delimited by the following coordinates: 49°16'59" – 49°19'03" N and 20°01'39"–20°05'22" E, in the range of altitudes between 920 and 1031 m a.s.l. (lower mountain zone).

A single plot consisted of 20 numbered living Norway spruces (240 in total) that were regularly checked during the growing season in order to identify and register the successively appearing trees infested by *I. typographus*. Some of them were then examined in order to acquire the main parameters of infestation, such as the infestation density, the sex ratio and effective reproduction rate, as the traits that could indicate the outbreak tendencies of the observed population (Lobinger 1996; Grodzki et al. 2006c, 2014; Grodzki and Gąsienica Fronek 2017b). For this purpose, two procedures were applied, depending on the nature protection status. In active protection zone, the selected trees were felled and then the bark samples 25 × 25 cm were taken from 4 section of the stem: I – in the stem base, II – midway between stem base and crown base, III – just under the crown, IV – in the middle of the crown (Grodzki 2007). In passive protection zone, the samples from section I and II were taken from the standing trees. The following parameters were registered on each bark sample:

- the bark thickness,
- the infestation density, understood as the number of mating chambers per 1 dm^2,
- the number of gallery systems with 1–4 maternal galleries,
- the sex ratio (mating chamber as the number of males, maternal galleries as the number of females),

– the length of maternal galleries (10 randomly chosen on each sample),
– effective reproduction rate (number of progeny – laid eggs and developing larvae),
– mortality (parasitoids, entomopathogenic fungi).

Additionally, the occurrence of accompanying bark beetle species and number of *Pityogenes chalcographus* (L.) gallery systems were recorded. Each tree was measured (DBH, length/height). The field survey was started on 10 April and continued till mid-September.

The statistical data treatment was aimed to test the significance of differences in the analysed traits using the one-way ANOVA and Pearson correlations for gallery length and number of progeny. For data processing, MSExcel and Statistica 9.0 (StatSoft Inc. 2009) were used.

Results

Tree mortality

During the growing season 2018, a total of 155 spruces (64% of initial number) infested by *I. typographus* were recorded on all 12 plots. On the plots under passive protection, 118 out of 120 trees (98%) were infested at the beginning of the growing season (between 19 and 29 April) and remaining 2 were not infested till the autumn. On the plots under active protection, 37 trees (31%) were infested – 30 between 19 and 25 April, and 7 between 27 July and 2 August; the others stayed alive till the autumn. During the sampling at the end of June, the pupae and young beetles were found in the galleries.

Traits of *I. typographus* population on infested trees

During the growing season in 2018, a total of 47 infested spruces were sampled: 17 trees in active protection zone (4 samples from each tree, 68 in total) and 30 trees in passive protection zone (2 samples from each tree, 60 in total). Mean (± SD) infestation density calculated from all 128 samples was 1.07 (± 0.48), being higher in passive (1.23 ±0.42) than in active (0.92 ±0.48) protection zone. On the trees sampled in 4 sections in active protection zone, the infestation density was the highest in section I (1.14 ± 0.35) and gradually decreased in higher tree sections, reaching 0.74 ± 0.51 in section IV (Fig. 1). On the trees sampled in the two sections in passive protection zone, the infestation density was lower in section I (0.14 ± 0.42) and slightly higher in section II (1.33 ± 0.37). The average values calculated for those two sections were higher on the plots under passive than under active protection (1.23 ± 0.42 and 1.03 ± 0.44, respectively) and differed significantly (ANOVA $F = 4.67$; $p < 0.05$; Fig. 1).

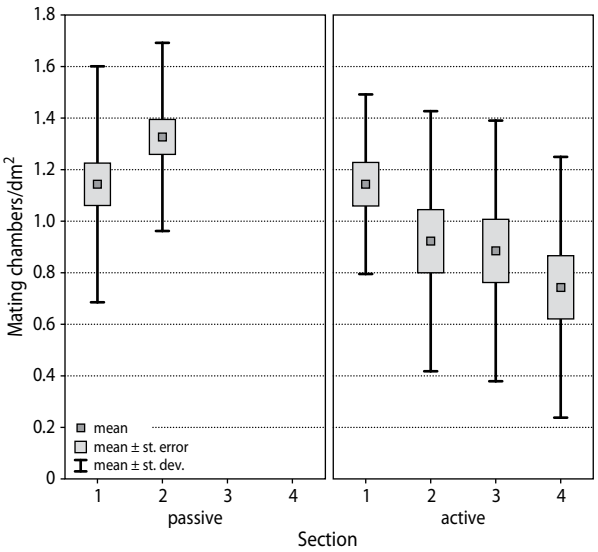

Figure 1. Infestation density in tree sections in passive and active protection zone

The bark thickness in analysed samples ranged between 2 and 8 mm (4.63 mm in average), although in the majority (89%) of samples, it was between 2 and 5 mm, and the bark thicker than 7 mm was found in only 4 cases (out of 128). No relationship between the bark thickness and the infestation density by *I. typographus* was found.

In the total set of 1709 analysed *I. typographus* gallery systems, those with 2 maternal galleries prevailed (63.0%), those with 1 maternal gallery were quite numerous (30.6%); however, the systems with 3 maternal galleries were very scarce, and with 4 – totally absent, regardless the protection status of the plot (Fig. 2).

The mean share of females defined based on the samples from 47 trees was 61.3 ± 12.8%, being higher in passive (63.1 ± 3.4%) than in active protection zone (59.6 ± 17.2%). When comparing the data from sections I and II only, the share of females was slightly higher in passive than in active protection zone (63.1 ± 3.4%

and 62.5 ± 12.4%, respectively), but with no significant differences.

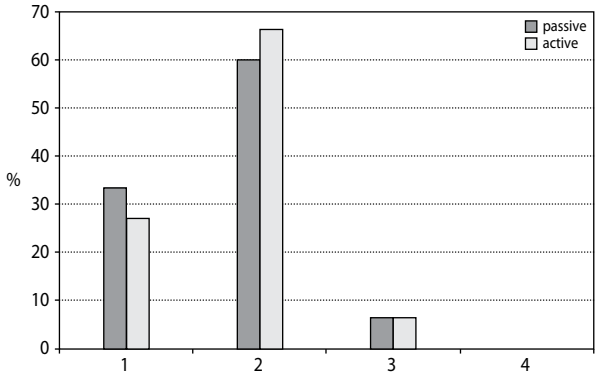

Figure 2. Share of gallery systems with 1–3 maternal galleries in tree sections in passive and active protection zone

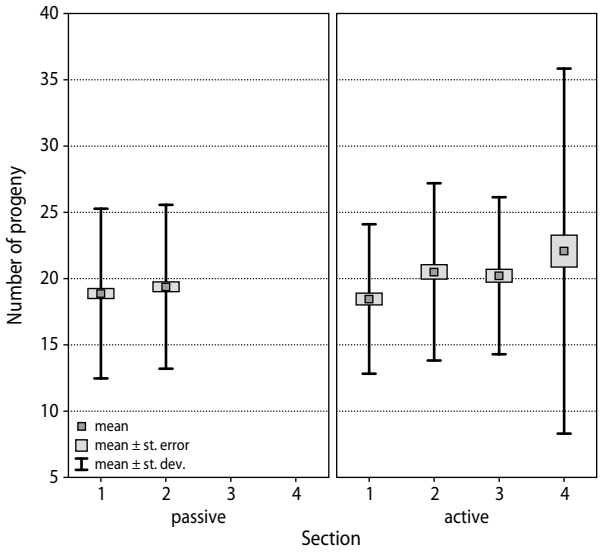

Figure 3. Mean number of progeny from 1 female in tree sections in passive and active protection zone

The average maternal gallery length of *I. typographus*, calculated from all analysed samples, was 63.6 ± 15.1 mm and was higher in the plots in passive than in active protection zone (64.4 ± 15.4 and 62.8 ± 14.8 mm, respectively), with no significant difference. The maternal gallery length decreased with increasing number of maternal galleries in a gallery system, and this effect was significant (ANOVA $F = 16.8$; $p < 0.001$). The maternal gallery length was slightly negatively correlated with the infestation density in analysed tree section ($r = –0.13$; $p < 0.001$).

The mean number of progeny per one female, calculated from all samples, was 16.69 ± 7.57, being higher in active than in passive protection zone (20.23 ± 8.49 and 19.12 ± 6.29, respectively). This value varied between individual sections of the tree, being the lowest in section I and then increasing gradually in sections II–IV (fig. 3). The number of progeny was slightly negatively correlated with the infestation density in the tree section ($r = -0.14$; $p < 0.001$).

Accompanying and antagonistic insects

In 58.6% of the analysed tree sections, the galleries of the bark beetle *Pityogenes chalcographus* (L.) were detected in average density 0.74 per 1 dm^2, the most frequently in sections II–IV (68–76%). One tree was infested by *Polygraphus poligraphus* (L.) in sections II–III. In 7 out of 128 analysed sections the cocoons of *Coeloides bostrychorum* (Gir.) (Hym., Braconidae) were found at the level of 2–15% of *I. typographus* young generation.

Discussion

The wind damage events, that affected the Norway spruce stands in the Tatra in the past, in most of the cases were acting as the inciting factor for the subsequent bark beetle outbreaks (Lindelöw and Schroeder 1998; Göthlin et al. 2000; Meier et al. 2003; Grodzki and Guzik 2009; Mezei et al. 2014; Grodzki and Gąsienica Fronek 2018). Similar mechanism, started by the wind damage from the spring 2017, is observed at present in the stands of the central/eastern part of the Tatra NP, where the presented research was conducted. The obtained results indicate the beginning of a new *I. typographus* outbreak, similar as in the eastern part of the Park after the wind damage from 2002 (Grodzki et al. 2006b), and according the pattern known from numerous cases across Europe (see references above).

The mortality level of Norway spruces in the observation plots established in 2018 was very high, and the infestation of individual trees by the beetles started very early. During the earlier survey conducted in the Kościeliska Valley (western part of the Park) in 2015, the first infested trees appeared in the third dec-

ade of July, and in 2016 – in the mid-June (Grodzki and Gąsienica Fronek 2017a). In the stands observed in 2018, the presence of infested trees in considerable number was detected in the third decade of April, and in the end of June the young beetles were found in the galleries. The lack of new infested trees on the plots with non-processed broken and fallen trees resulted from the fact that all the numbered spruces were attacked by the beetles during the first wave of spring swarming. Contrarily, on the plots subjected to active protection (where windblown trees were removed), the intensity of infestation by the beetles during first and next waves of swarming was much lower. This indicates that the undertaken activities aimed to the reduction of breeding material suitable for *I. typographus* reproduction have a positive effect, as it was earlier in the Kościeliska Valley (Grodzki and Gąsienica Fronek 2017a) and in the other stands affected by wind (Schroeder and Lindelöw 2002; Forster et al. 2003).

The infestation density on the trees analysed in 2018 was high, much higher than the values recorded in the Kościeliska Valley in 2015–2017 (Grodzki and Gąsienica Fronek 2017a) and in the stands in Beskid Śląski in 2002 during retrogradation phase (Grodzki 2004), but close to these noted in the Tatra in 2000–2001 (Grodzki et al. 2002). High infestation density found in 2018 indicates relatively high resistance of spruces attacked by *I. typographus* (Christiansen et al. 1987), as it was observed earlier in the wind-damaged stands in the Tatra (Grodzki et al. 2007; Mezei et al. 2014).

The share of females in 2018 (61%) was similar to the level recorded in the Kościeliska Valley in 2015–2016 (63–64%), thus indicating the tendency for further development of *I. typographus* outbreak (Lobinger 1996; Grodzki and Gąsienica Fronek 2017b). The share of females in the populations attacking spruces in Tatra, Gorce and Beskid Żywiecki during progradation and culmination phase of the outbreak was slightly higher, reaching 64–69% (Grodzki et al. 2006b, 2007, 2014). On the other hand, the effective reproduction rate in 2018 (19.7 eggs/larvae per 1 female) was lower than in the Kościeliska Valley in the first year of the outbreak (27.4 eggs/larvae per 1 female), but higher than the mean value calculated using the models based on field data (Grodzki and Gąsienica Fronek 2017b); nevertheless, the high infestation density and early started development of pre-imaginal stages in the spring indicate the risk of fast increase in *I. typographus* population level in this newly appearing outbreak area. Also, the increasing frequency of *P. chalcographus*, an important bark beetle species that contributes to the spruce mortality (Grodzki 1997, 2004), as well as low level of parasitism, should be seen as additional factors that affect the threat to those stands.

In the recent years, the usefulness and effectiveness of active protection measures aimed to the mitigation of *I. typographus* outbreaks is often considered as controversial (e.g. Fahse and Heurich 2011; Temperli et al. 2014), especially in the areas under (active) nature protection (e.g. Müller et al. 2008; Markovic and Stojanovic 2010; Hilszczański and Starzyk 2017).

The results of the field survey done in 2014–2017 in the Kościeliska Valley revealed the fast development of *I. typographus* outbreak in the stands affected by the wind in 2013, but also the positive effect of the active protection procedures applied just after the damage, that was nullified later, when the protection measures have been abandoned (Grodzki and Gąsienica Fronek 2018). Similar, although somehow reduced due to bark beetle migration between closely located stands (Gries 1985), positive effect of active protection expressed by lower mortality of spruces infested by the bark beetles in the stands subjected to the processing and removal of broken and fallen trees, was observed during the presented survey. This indicated once again that the application of forest protection measures aimed for the reduction of breeding resources and mitigation of *I. typographus* reproduction, formally allowed in the zone of active nature protection, is justified and useful, as it was demonstrated based on the observations from previous bark beetle outbreaks in the Tatra (Grodzki et al. 2006a; Grodzki and Guzik 2009; Mezei et al. 2017; Grodzki and Gąsienica Fronek 2017a).

Conclusions

– The results of 2018 survey from the wind-damaged spruce stands in the eastern part of the Tatra National Park indicate the beginning of recurrent *I. typographus* outbreak, according to the pattern known earlier from the other areas in Poland and Europe, and recently described in Kościeliska Valley in 2014–2017.

- In the weather conditions of the spring 2018, the infestation of spruces by *I. typographus* started very early and was very dynamic, which positively affected the reproduction abilities of the beetle during the whole growing season.
- *I. typographus* attack on standing trees had lower intensity in the stands previously subjected to the processing and removal of fallen and broken trees, which indicates the positive effect of implemented active protection procedures.
- The parameters describing *I. typographus* population on attacked trees, as well as low activity of natural enemies, indicate its reproduction potential and high risk of the development of a new outbreak.
- Similar level of those parameters in the plots under active and passive protection regime can result from their neighbourhood, but indicates high threat caused by *I. typographus* to all stands in this area, regardless their protection status.

Acknowledgements and source of funding

Research was done within the project called 'Impact of forestry treatments in the spruce stands of the Tatra National Park on the occurrence of cambiophagus insects' accomplished in 2018 by the Tatra National Park and financed from the resources of the Polish State Forests Forest Fund.

References

Christiansen, E., Waring, R.H., Berryman, A.A. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. *Forest Ecology and Management*, 22, 89–106. DOI: 10.1016/0378-1127(87)90098-3

Fahse, L., Heurich, M. 2011. Simulation and analysis of outbreaks of bark beetle infestations and their management at the stand level. *Ecological Modelling*, 222 (11), 1833–1846. DOI: 10.1016/j.ecolmodel.2011.03.014

Forster, B., Meier, F., Gall, R. 2003. Bark beetle management after a mass attack – some Swiss experiences. In: Proceedings Ecology, Survey and Management of Forest Insects (eds.: M. McManus, A. Liebhold). USDA Forest Service, Northeastern Research Station, General Technical Report NE-311, 10–15.

Göthlin, E., Schroeder, L.M. Lindelöw, A. 2000. Attacks by *Ips typographus* and *Pityogenes chalcographus* on windthrown spruces (*Picea abies*) during the two years following a storm felling. *Scandinavian Journal of Forest Research*, 15 , 542–549. DOI: 10.1080/028275800750173492

Gries, G. 1985. Zur Frage der Dispersion des Buchdruckers (*Ips typographus* L.) (in German with English summary). *Zeitschrift für Angewandte Entomologie*, 99, 12–20. DOI: 10.1111/j.1439-0418.1985.tb01953.x

Grodzki, W. 1997. Changes in the occurrence of bark beetles on Norway spruce in a forest decline area in the Sudety Mountains in Poland. In: Proceedings of the IUFRO conference, Integrating cultural tactics into the management of bark beetles and reforestation pests, Vallombrosa 1–4 September 1996 (eds.: J.-C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, S.M. Salom). USDA, Forest Service General Technical Report NE-236, 105–111.

Grodzki, W. 2004. Threat to Norway spruce stands of insect pests in the western part of Beskidy mountains (in Polish with English summary). *Leśne Prace Badawcze*, 2, 35–47.

Grodzki, W. 2007. The use of pheromone traps for the monitoring of *Ips typographus* (L.) populations in selected national parks in the Carpathians (in Polish with English summary). *Prace Instytutu Badawczego Leśnictwa, Rozprawy i monografie*, 8, 1–127.

Grodzki, W., Gąsienica Fronek, W. 2017a. Occurrence of *Ips typographus* (L.) after wind damage in the Kościeliska Valley of the Tatra National Park. *Leśne Prace Badawcze*, 78 (2), 113–119. DOI: 10.1515/frp-2017-0012

Grodzki, W., Gąsienica Fronek, W. 2017b. Reproduction abilities of *Ips typographus* (L.) (Coleoptera: Curculionidae, Scolytinae) in the stands damaged by the wind in 2013 in the Kościeliska Valley (Tatra National Park). *Folia Forestalia Polonica, Series A – Forestry*, 59 (4), 259–264. DOI: 10.1515/ffp-2017-0027

Grodzki, W., Gąsienica Fronek, W. 2018. Effect of forest protection strategy on the occurrence of

the spruce bark beetle *Ips typographus* (L.) in the Kościeliska Valley in the Tatra National Park. *Sylwan*,162 (8), 628−637. DOI: 10.26202/sylwan.2018032

Grodzki, W., Guzik, M. 2009. Wind- and snow damage and the spruce bark beetle outbreaks in the Tatra National Park during last 100 years. Attempt to spatial characteristics. In: Long-term changes in the nature and use of the TNP area (in Polish) (ed.: M. Guzik). TPN Zakopane, 33–46.

Grodzki, W., Jakuš, R., Lajzová, E., Sitková, Z., Mączka, T., Škvarenina J. 2006a. Effects of intensive versus no management strategies during an outbreak of the bark beetle *Ips typographus* (L.) (Col.: Curculionidae, Scolytinae) in the Tatra Mts. in Poland and Slovakia. *Annals of Forest Science*, 63: 55–61. DOI: 10.1051/forest:2005097.

Grodzki, W., Loch, J., Armatys, P. 2006b. Occurrence of *Ips typographus* L. in wind-damaged Norway spruce stands of Kudłoń massif in the Gorce National Park. (in Polish with English summary). *Ochrona Beskidów Zachodnich*, 1, 125–137.

Grodzki, W., McManus, M., Knížek, M., Meshkova, V., Mihalciuc, V., Novotny, J., Turčani, M., Slobodyan, Y. 2002. The response of *Ips typographus* (L.) populations in polluted and non-polluted spruce stands in the Carpathian Mountain region. [In:] Effects of Air pollution on Forest Health and biodiversity in Forests of the Carpathian Mountains. Robert C. Szaro, A. Bytnerowicz and J. Oszlanyi (eds.)., IOS Press, NATO Science Series, Series I – Life and Behavioural Sciences, Vol. 345, Amsterdam. 236–249.

Grodzki, W., Starzyk, J.R., Kosibowicz, M. 2006c. Windthrowns and cambiophagous insects and the problems with the protection of spruce stands in the Tatra National Park. In: The nature of the Tatra National Park and man. Part II – Biological sciences (in Polish) (eds.: Z. Mirek, B. Godzik). TPN – PTPNoZ, Zakopane – Kraków, 115–124.

Grodzki, W., Starzyk, J.R., Kosibowicz, M. 2014. Variability of selected traits of *Ips typographus* (L.) (Col.: Scolytinae) populations in an area affected by bark beetle outbreak in Beskid Żywiecki (Western Carpathians, Poland). *Folia Forestalia Polonica, Series A – Forestry*, 56 (2), 79–92. DOI 10.2478/ffp-2014-0008

Grodzki, W., Starzyk, J.R., Kosibowicz, M., Michalcewicz, J., Mączka, T. 2007. Effect of wind damage on the populations of cambiophagous insects and threat to Norway spruce stands in the Tatra National Park. Final report of the project 2 P06L 046 27 (in Polish). Instytut Badawczy Leśnictwa, manuscript.

Hilszczański, J., Starzyk, J.R. 2017. Is it possible and necessary to control European spruce bark beetle *Ips typographus* (L.) outbreak in the Białowieża Forest? *Leśne Prace Badawcze*, 78 (1), 88–92. DOI: 10.1515/frp-2017-0009

Lindelöw, A., Schroeder, L.M. 1998. Spruce bark beetle (*Ips typographus*) attack within and outside protected areas after a stormfelling in November 1995. In: Methodology of forest insect and disease survey in Central Europe. Proceedings, First Workshop of the IUFRO WP 7.03.10, Ustroń – Jaszowiec (eds.: W. Grodzki, M. Knížek, B. Forster). IUFRO – Forest Research Institute, Warsaw, 177–180.

Lobinger, G. 1996. Variations in sex ratio during outbreak of *Ips typographus* (Col., Scolytidae) in Southern Bavaria. *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz*, 69, 3, 51–53.

Markovic, C., Stojanovic, A. 2010. Differences in bark beetle (*Ips typographus* and *Pityogenes chalcographus*) abundance in a strict spruce reserve and the surrounding spruce forests of Serbia. *Phytoparasitica*, 38, 31–37. DOI: 10.1007/s12600-009-0076-x

Meier, F., Gall, R., Forster, B. 2003. Ursachen und Verlauf der Buchdrucker-Epidemien (*Ips typographus* L.) in der Schweitz von 1984 bis 1999. *Schweizerische Zeitschrift für Forstwesen*, 11, 437–441.

Mezei, P., Blaženec, M., Grodzki, W., Jakuš, R. 2017. Influence of different forest protection strategies on spruce tree mortality during a bark beetle outbreak. *Annals of Forest Science*, 74. DOI 10.1007/s13595-017-0663-9

Mezei, P., Grodzki, W., Blaženec, M., Jakuš, R. 2014. Factors influencing the *wind–bark beetles*' disturbance system in the course of an *Ips typographus* outbreak in the Tatra Mountains. *Forest Ecology and Management*, 312, 67–77. DOI: 10.1016/j.foreco.2013.10.020

Müller, J., Bußler, H., Goßner, M., Rettelbach, T., Duelli, P. 2008. The European spruce bark beetle *Ips*

typographus in a national park: from pest to keystone species. *Biodiversity and Conservation*, 17, 2979–3001. DOI: 10.1007/s10531-008-9409-1

Schroeder, L.M., Lindelöw, Å. 2002. Attack on living spruces by the bark beetle *Ips typographus* (Col. Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind−felled trees. *Agricultural and Forest Entomology*, 4, 47–56.

StatSoft Inc., 2009. STATISTICA for Windows (Computer program manual). Tulsa, OK: StatSoft, Inc., http://www.statsoft.com

Temperli, C., Hart, S., Veblen, T.T., Kulakowski, D., Hicks, J., Andrus, R. 2014. Are density reduction treatments effective at managing for resistance or resilience to spruce beetle disturbance in the southern Rocky Mountains? *Forest Ecology and Management*, 334, 53–63. DOI: 10.1016/j.foreco.2014.08.028