

Variability of selected traits of *Ips typographus* (L.) (Col.: Scolytinae) populations in Beskid Żywiecki (Western Carpathians, Poland) region affected by bark beetle outbreak

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ABSTRACT

In 2010–2012, investigations on *Ips typographus* populations were carried out in Norway spruce stands recently affected by bark beetle outbreak in the Beskid Żywiecki Mts. in Poland. The aim of the study was to test the usefulness of several traits describing *I. typographus* populations for evaluation of their actual outbreak tendency. Infestation density, sex ratio, gallery length, progeny number and beetle length were used as the traits. Trait variability was analyzed in relation to infested tree mortality in the current year of observation and outbreak tendency defined by the comparison of data on tree mortality in the current year and that in the year before.

The highest infestation density was found in the stands representing the highest tree mortality in the current year and in those characterized by decreasing outbreak tendency. The gallery system with 2 maternal galleries dominated. The sex ratio of attacking beetles inclined towards females (63.8%) and remained stable during 3 years of observations; the highest percentage of females was found in locations being in stabilization/latency outbreak phase. The length of maternal galleries was somewhat negatively affected by infestation density and positively correlated with the number of progeny in the gallery. The average beetle length was 4.800 mm (± 0.293), ranging between 3.718 and 5.817 mm and being the highest in the uppermost class of tree mortality recorded in the current year of observation. The shortest beetles were collected in the stands with increasing outbreak tendency, and slightly longer – in the stands with outbreak stable and decreasing tendencies.

None of the traits tested can be selected as a direct indicator for prediction of outbreak tendency in *I. typographus* populations. Possible reasons of variability in the analyzed traits are discussed. The traits indicate that *I. typographus* in the study area represent very high reproductive potential, thus the risk of repeated outbreak is very high.

KEY WORDS

bark beetles, galleries, progeny, sex ratio, body length, population dynamics

INTRODUCTION

In the Western Carpathians, starting from 2002, an extended bark beetle *Ips typographus* (L.) outbreak developed in Norway spruce *Picea abies* (L.) H. Karst. stands growing in the Beskid Śląski (earlier) as well as the Beskid Żywiecki mountains (later) and culminated in 2007–2008. The outbreak generally started in the lower mountain zone, in Norway spruce stands already affected by root rott (*Armillaria* spp.), and then spread towards higher altitudes up to mountain crests (Grodzki 2010). The outbreak course, however, was not spatially homogenous, thus at a certain point of time it seemed possible to distinguish some sub-areas representing various outbreak phases.

It is known that population dynamics of bark beetles in Norway spruce stands depends on several environmental factors resulting from site and stand characteristics (Netherer and Nopp-Mayr 2005). However, an analysis of these factors in the Beskid Żywiecki revealed that under outbreak conditions, the patterns describing bark beetle preferences seemed to be not as distinctive as those known from preceding studies (Grodzki *et al.* 2014). On the other hand, knowledge on *I. typographus* population traits with respect to outbreak tendencies of this species has not been yet completed. It is recognized that population sex ratio varies in particular outbreak stages and the percentage of females is higher in progradation phase (Lobinger 1996). Other parameters, such as: infestation density and gallery length (Anderbrant 1990; Anderbrant and Schlyter 1989), body size or dry weight of adults (Atkins 1975), elytra weight (Botterweg 1983), length of beetles (Grodzki 2004) or several biometric measures of adults (Sallé *et al.* 2005) have been so far used to characterize *I. typographus* populations in relation to various breeding conditions. Yet, for the most part knowledge gained requires further tests and/or verification in outbreak conditions in Central European *P. abies* forests.

The aim of this study was to explore various traits describing populations of the spruce bark beetle *I. typographus* infesting Norway spruce trees in order to determine trait variability patterns connected with pest population status and outbreak tendency. Information obtained might be very useful in risk assessment and prediction of bark beetle populations' dynamics in the future.

MATERIALS AND METHODS

The investigations were done in 2010–2012. The study area extended in the Beskid Żywiecki (Western Carpathians, Poland) within a range of three Forest Districts: Jeleśnia, Ujszoły and Węgierska Górka (49°23'42" – 49°38'54" N; 18°58'29" – 19°27'16" E) affected by *I. typographus* outbreak to different degrees. Generally, based on historical data, the Forest Districts Ujszoły and Węgierska Górka could be defined as the area in outbreak retrogradation phase, and Jeleśnia – in stabilization/latency phase with relatively lower bark beetle population numbers (Grodzki *et al.* 2014).

Field investigations were carried out on research plots temporarily established in Norway spruce stands. The plots (32) represented the parts of stands, where dying or dead trees already infested by *I. typographus* were felled and dissected. Additionally, bark beetles for body measurements were sampled from pheromone traps situated in 35 localities. In some cases the pheromone traps were installed within plot locations, which enabled comparisons of beetles collected from the traps and from under the bark of dissected trees. The plots and traps were georeferenced using GPS receiver (fig. 1) in order to precisely assign field results to data, concerning tree mortality in corresponding sub-compartments taken from the State Forests' database. Three classes of bark beetle-related Norway spruce mortality were defined based on the yearly volume of infested trees per 1 ha: I – < 5 m³, II – 5–10 m³, III – > 10 m³ in a given sub-compartment and used in further analyses.

The parameters describing selected traits of bark beetle populations in the parts of infested trees were assessed using 3 half-meter-long sections of the stem, located in its distinctive zones: I – at the stem base, II – midway between the stem base and crown base, III – under the crown base (Grodzki 2007, modified). The sections were selected and marked after tree felling, when the circumference was measured with the aim to calculate the surface of analyzed bark. The following features were registered in each stem section:

- infestation density (the number of gallery systems including those with 1, 2, 3 or 4 maternal galleries),
- sex structure of bark beetle population infesting analyzed trees, using the number of nuptial chambers as the number of males and the number of maternal galleries as the number of females,

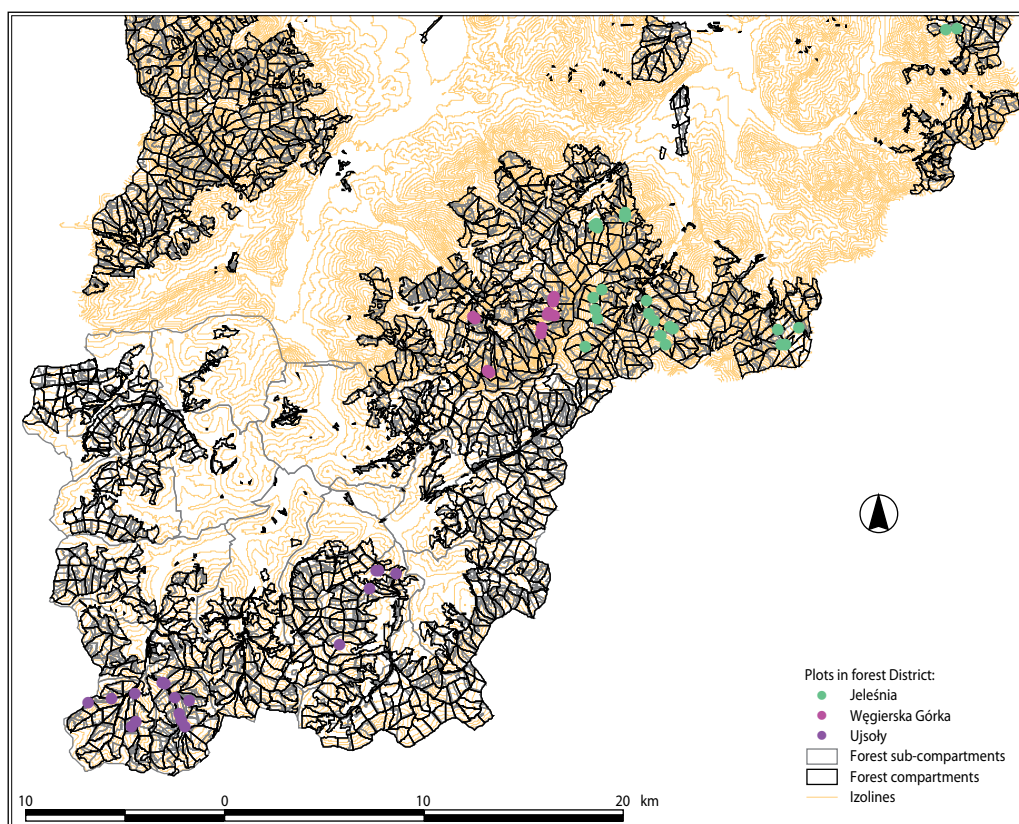


Figure 1. Location of research sites in the Beskid Żywiecki (Forest Districts: Jeleśnia, Węgierska Górka and Ujsoly)

- the length of maternal galleries – 10 galleries were randomly chosen from the systems with 1–4 females and measured,
- effective reproduction understood as the number of eggs and larvae per one maternal gallery.

The measurements of *I. typographus* body length were performed by means of the image analysis method using a flatbed scanner and software for accurate measurements WinSEEDLE (Regent Instruments Canada Inc.). The bark beetles were collected in June-July from Theysohn traps baited with Ipsodor (ZD Chemipan, Poland). The beetles, after storing in ethanol, were dried before measurements and then undamaged individuals with closed elytrae were organized in 100-specimen samples and placed on dorsal side on scanner glass and then automatically measured.

The parameters describing *I. typographus* populations in individual study plots were related to bark beetle-related tree mortality in individual sub-compartments in a given year, with outbreak tendency defined

by the comparison of data on tree mortality in the current year of observation and that observed in the year before, reflecting outbreak phase. Tree mortality was assessed using data taken from the State Forests' IT system (SILP) as regards the volume of trees infested by bark beetles and felled within a given year in the individual forest sub-compartment. Definite outbreak tendency (increasing – decreasing – stable) in a given sub-compartment was determined by the comparison of the volume of infested trees per 1 ha, felled in the year of analyses and the year before. Statistical data treatment aimed to test significance of differences in the traits analyzed using: nonparametric Kruskal-Wallis (K-W) test for infestation density, characteristics of galleries and sex structure of attacking beetles, K-W test and Pearson correlations for gallery length and the number of progeny, and K-W test along with one-way ANOVA for body length of beetles. For data processing there were used MSEXcel with XLSTAT 2012 (Addinsoft) and Statistica 5.0 (StatSoft Inc. 2009).

RESULTS

Infestation density and characteristics of galleries

In total, 321 sections from 107 infested trees on 32 locations were analyzed. Mean (\pm SD) density of gallery systems (mating chambers per dm^2) in 285 infested stem sections during the whole 3-year period was 0.570 (± 0.425) and varied in a range between 0.13 and 1.02 mating chambers per dm^2 on individual plots.

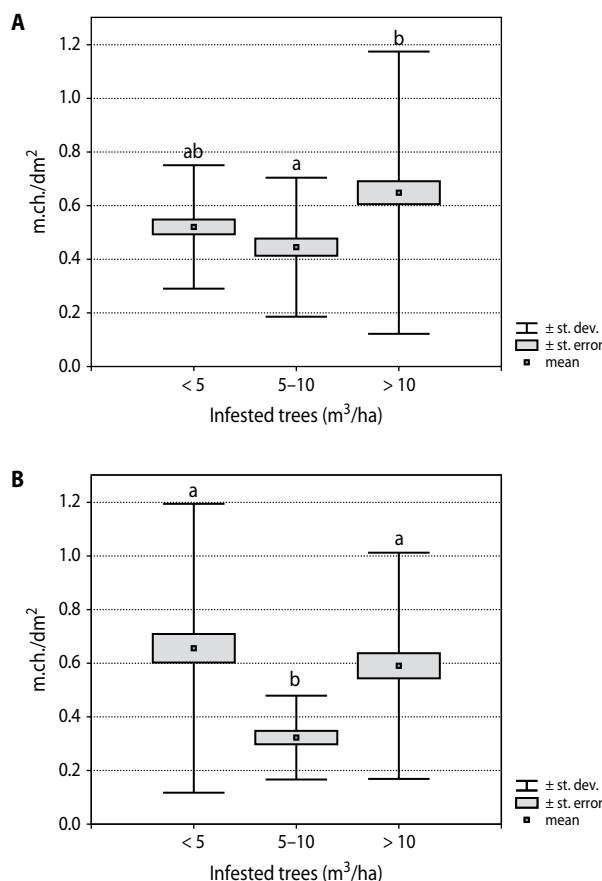


Figure 2. Density of *I. typographus* mating chambers in analyzed Norway spruce stem sections in 2010–2012 with respect to volume of trees infested in the year before analysis (A) and in the current year (B)

Infestation density varied significantly in relation to attack intensity expressed by the volume of infested trees per 1 ha in the previous [K-W $H(\text{DF} = 2, N = 285) = 7.64, p = 0.022$] and the current year of infestation [K-W $H(\text{DF} = 2, N = 222) = 22.48, p < 0.001$]. In case of the previous year infestation, the highest value

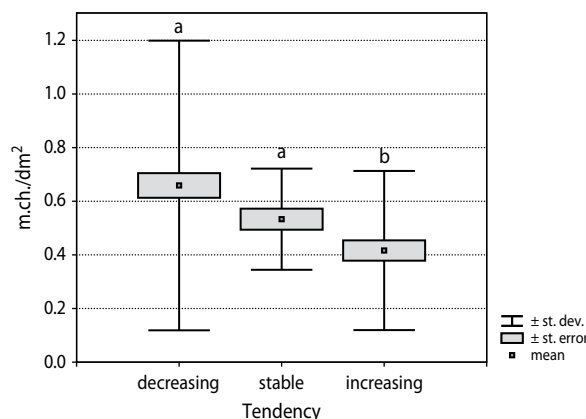


Figure 3. Density of *I. typographus* mating chambers in analyzed Norway spruce stem sections in 2010–2012 with respect to outbreak tendency

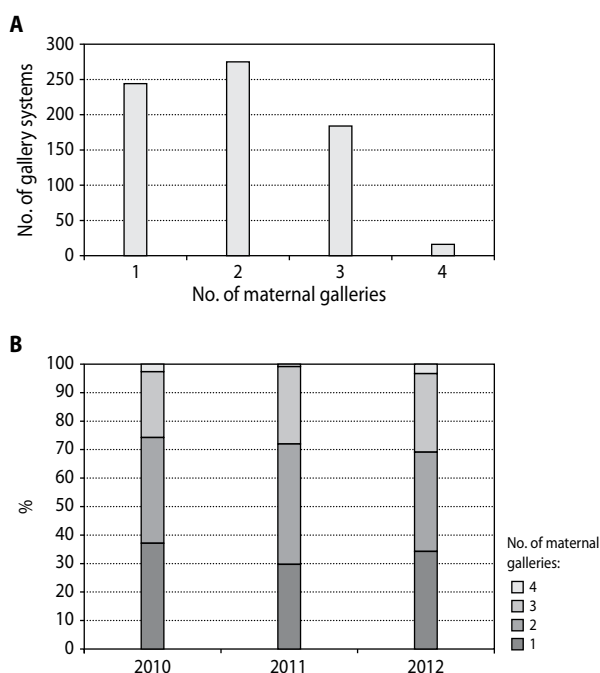
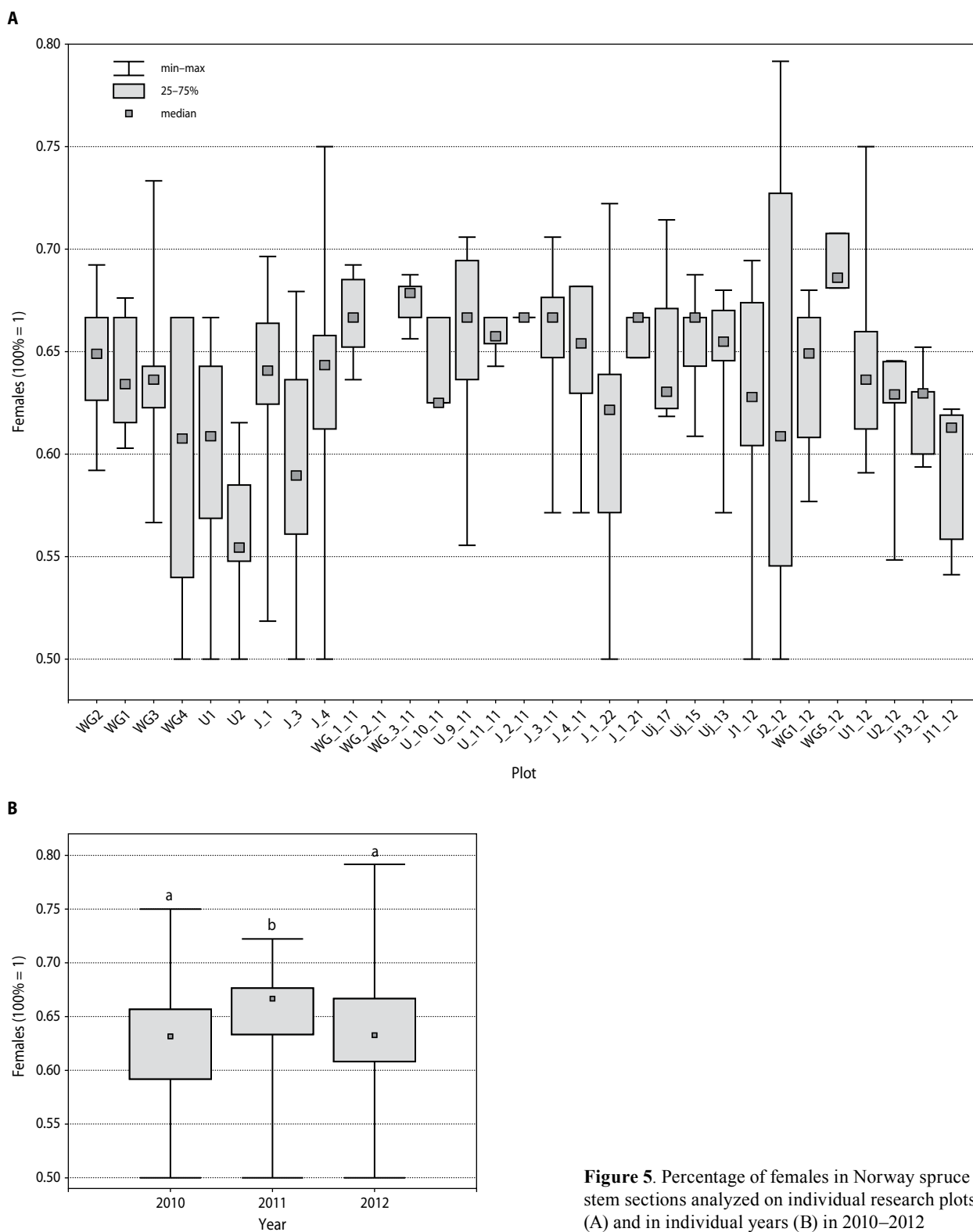


Figure 4. Number of gallery systems with 1–4 maternal galleries in analyzed Norway spruce stem sections (A) and percentage of systems with 1–4 females in 2010–2012 (B)

of infestation density was found in the stands representing the highest (III) class of tree mortality and it significantly differed from that observed for the intermediate (II) class: ($p = 0.02$). In case of the current year of infestation, the highest values were observed in the stands representing the lowest (I) and highest (III) classes of tree mortality and they significantly ($p < 0.001$) dif-



ferred from those observed in the intermediate (II) class (fig. 2).

Infestation density was the highest in the stands representing decreasing outbreak tendency, and the lowest – in those with increasing tendency, but only the values attributed to increasing tendency differed significantly [K-W $H(DF = 2, N = 222) = 14.41, p < 0.001$] from others (fig. 3).

The gallery systems with 2 maternal galleries dominated in the stem sections analyzed, and 1 and 3 galleries were quite frequently found as well, whereas the systems with 4 maternal galleries were very rarely observed (fig. 4A). The percentage of the systems with a given number of maternal galleries was quite stable in subsequent years of the study (fig. 4B).

Sexual structure of attacking beetles

Mean ($\pm SD$) percentage of females in the populations infesting analyzed trees was $63.8\% \pm 5.02$ (sex ratio 1 : 1.82), varying strongly between the study sites and ranged from 55.9 to 69.2% (fig. 5). No statistically significant differences were found when comparing the data collected during 3 years on the plots located in the areas being in different outbreak phases (retrogradation, stabilization).

The percentage of females was significantly diverse between the years of investigations (K-W $H(DF = 2, N = 285) = 25.31, p < 0.001$), reaching significantly ($p < 0.001$) higher mean value in 2011 (65.1%) than in 2010 and 2012 (62.3 and 63.6%, respectively; fig. 6A). The percentage of females related to the volume of infested trees felled in the year before was the highest (65.0%) in the lowest (I) class of tree mortality, slightly lower (63.8%) in the highest (III) class and the lowest (62.2%) in the class of intermediate (II) mortality (fig. 6B), but the results differed significantly only between classes I and II ($p < 0.001$). The percentage of females decreased with increasing mortality of infested trees within the current year (fig. 6B), but significant differences ($p = 0.015$) were found only between classes I and III.

The sexual structure of *I. typographus* populations, analyzed in relation to outbreak tendency defined for each of the research plots, was also significantly diversified (K-W $H(DF = 2, N = 222) = 23.81, p < 0.001$). The highest share of females (67.1%) was found for stabilization/latency outbreak phase (fig. 7), whereas in case of both increasing and decreasing tendencies, female share

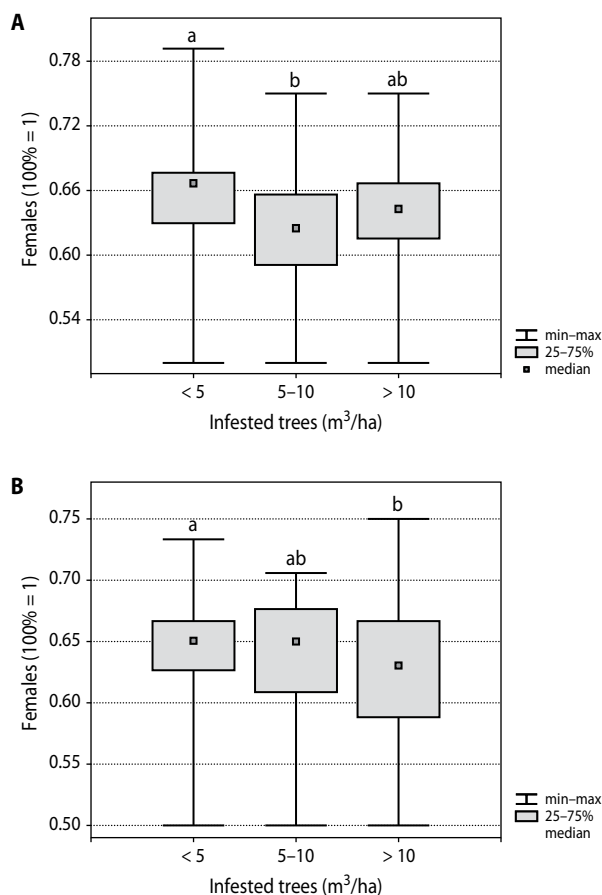


Figure 6. Percentage of females in stem sections of Norway spruces analyzed on research plots according to tree mortality in the year before analysis (A) and in the current year (B)

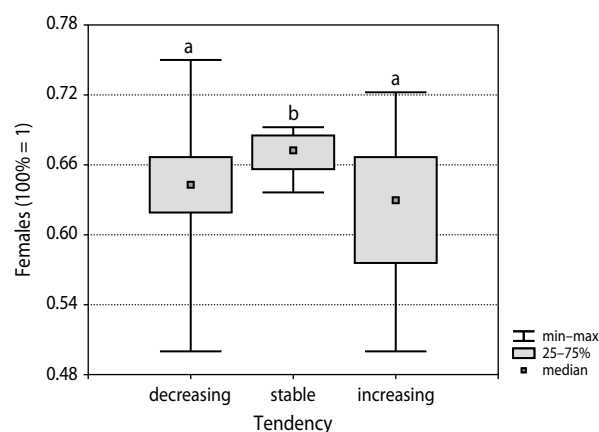


Figure 7. Percentage of females in Norway spruce stem sections analyzed on the plots with different outbreak tendency evaluated for the year of analysis

was lower (62.7 and 63.6%, respectively). Only the data assigned to stable outbreak phase differed significantly ($p < 0.001$) from those representing increasing and decreasing tendencies.

Gallery length and progeny

During 3-year-long research, there were measured in total 279 maternal galleries in 321 analyzed stem sections. Mean gallery length highly varied [K-W $H(DF = 23, N = 2004) = 227.20, p < 0.001$] between individual research sites (fig. 8). The average value was 6.75 cm with a range between 0.6 and 20.4 cm. The studied parameter varied upon the number of females starting from one mating chamber [K-W $H(DF = 3, N = 2004) = 26.07, p < 0.001$], and generally decreased with increasing number of females (fig. 9A), although the difference was statistically significant (at $p < 0.05$) in case of 2 and more females in the gallery system. Taking into account high percentage of the systems with 2–3 maternal galleries (fig. 4A), the decrease of gallery length with increasing number of females only somehow confirms the existence of intraspecific competition mechanism in *I. typographus*.

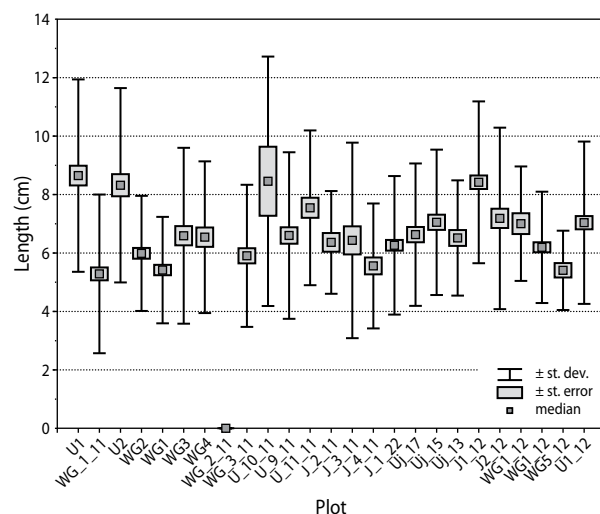


Figure 8. Length of maternal galleries in *I. typographus* gallery systems in Norway spruce trees analyzed on all plots in 2010–2012

Competition mechanisms (especially – spatial) affected the number of progeny in the gallery systems established with various number of females starting from the same mating chamber (fig. 9B). The mean number

of eggs or larvae in one maternal gallery was 21.4 with a range from 1 to 91. The number of eggs decreased with increasing numbers of females in one gallery system [K-W $H(DF = 3, N = 1998) = 46.80, p < 0.001$], however statistically significant differences at $p < 0.05$ were revealed only in case of 2 and more females in the gallery systems.

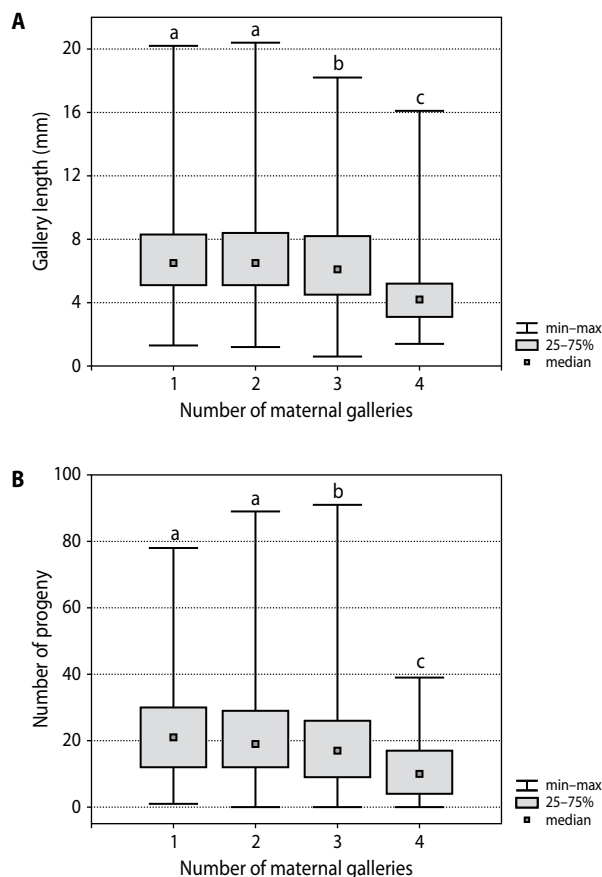


Figure 9. Length of maternal galleries (A) and the number of progeny (B) in the systems with 1–4 *I. typographus* females on all research sites in 2010–2012

The number of progeny (eggs and larvae) in one maternal gallery was positively correlated with its length ($r = 0.72$, $p < 0.001$, $N = 2050$) (fig. 10) and this relationship, found in all the study years, can be described by the following equation of regression:

$$y = 0.3376x - 1.4768$$

where: y is the number of progeny and x is gallery length.

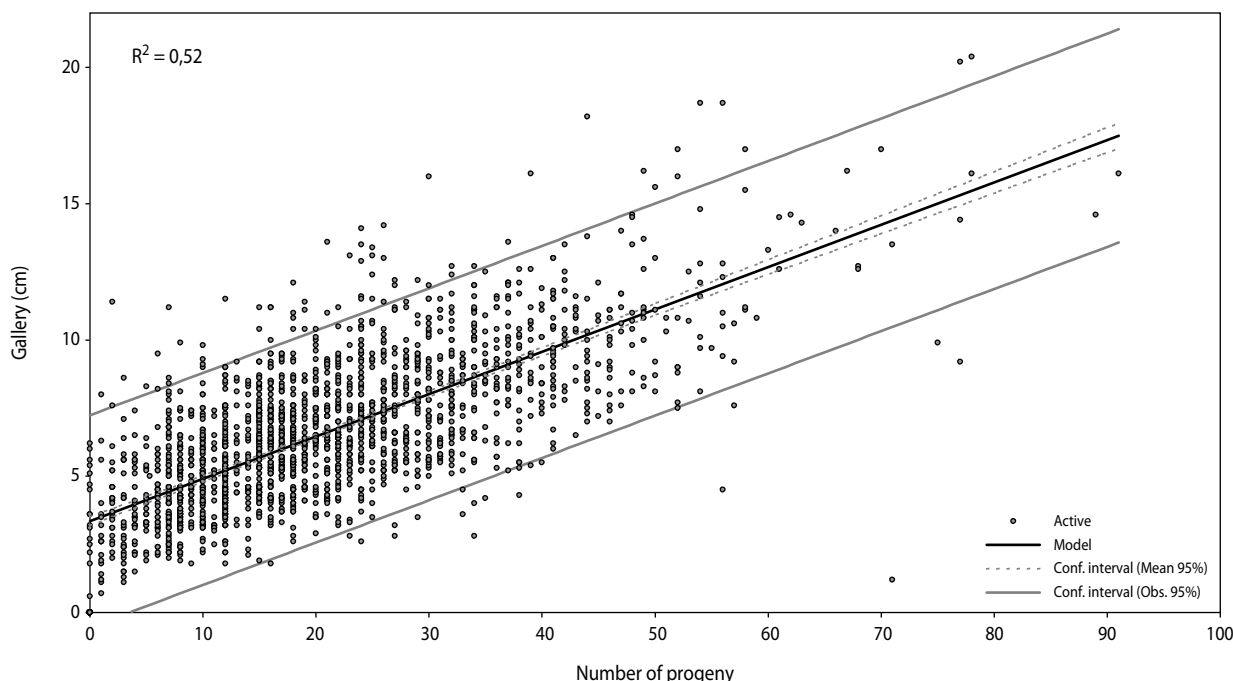


Figure 10. Relation between the number of progeny in maternal gallery and gallery length in analyzed spruce sections in 2010–2012

Density of galleries in the analyzed sections was found as a factor slightly limiting both the length of maternal galleries ($r = -0.14$, $p < 0.001$) and the number of progeny in a given gallery ($r = -0.09$, $p < 0.001$).

Body length of beetles

During 3 years of observations, in total 3234 *I. typographus* beetles were collected on 37 localities. The 100-beetle samples were usually used for measurements, except for some cases when beetles were collected from the galleries and then the sample size was smaller.

Distribution of the trait analyzed was normal. The average beetle length was 4.800 (± 0.293) mm, with a range between 3.718 and 5.817 mm. Differentiation between the samples collected from the localities observed was quite high [K-W $H(DF = 36, N = 3234) = 203.66$, $p < 0.001$]. The lowest mean body length value was 4.687 mm and the highest – 5.075 mm (fig. 11A). The mean values in samples collected from 16 localities representing 1410 beetles were above the overall average value, while the mean values in samples from 21 localities (1832 beetles) were below this value. No temporal or spatial pattern of body length variability was found.

No statistical differences (ANOVA $F = 0.90$, $p = 0.91$) were found for the years of observations (fig. 11B), thus pooled data were used for further analyses.

When analyzing relations between *I. typographus* body length and tree mortality, there were used data on the volume of trees infested by bark beetles in a given sub-compartment during the current year and the year before. The average length of beetles increased with increasing tree mortality in the current year [K-W $H(DF = 2, N = 3234) = 14.43$, $p < 0.001$], but the differences at $p < 0.05$ were shown only for mortality class I when compared with class II (fig. 12A). The beetle length related to tree mortality in the year before was less diversified [K-W $H(DF = 2, N = 1842) = 5.80$, $p < 0.05$], and had no pattern as defined for the current year tree mortality (fig. 12B).

The variability of beetle length in relation to outbreak tendency, defined for the sub-compartments where the beetles were collected, showed that the shortest beetles were collected in the stands with increasing outbreak tendency, and slightly longer – in case of those with stable and decreasing tendencies (fig. 13). However, the differences found were not statistically significant [K-W $H(DF = 2, N = 1842) = 2.33$, $p = 0.31$].

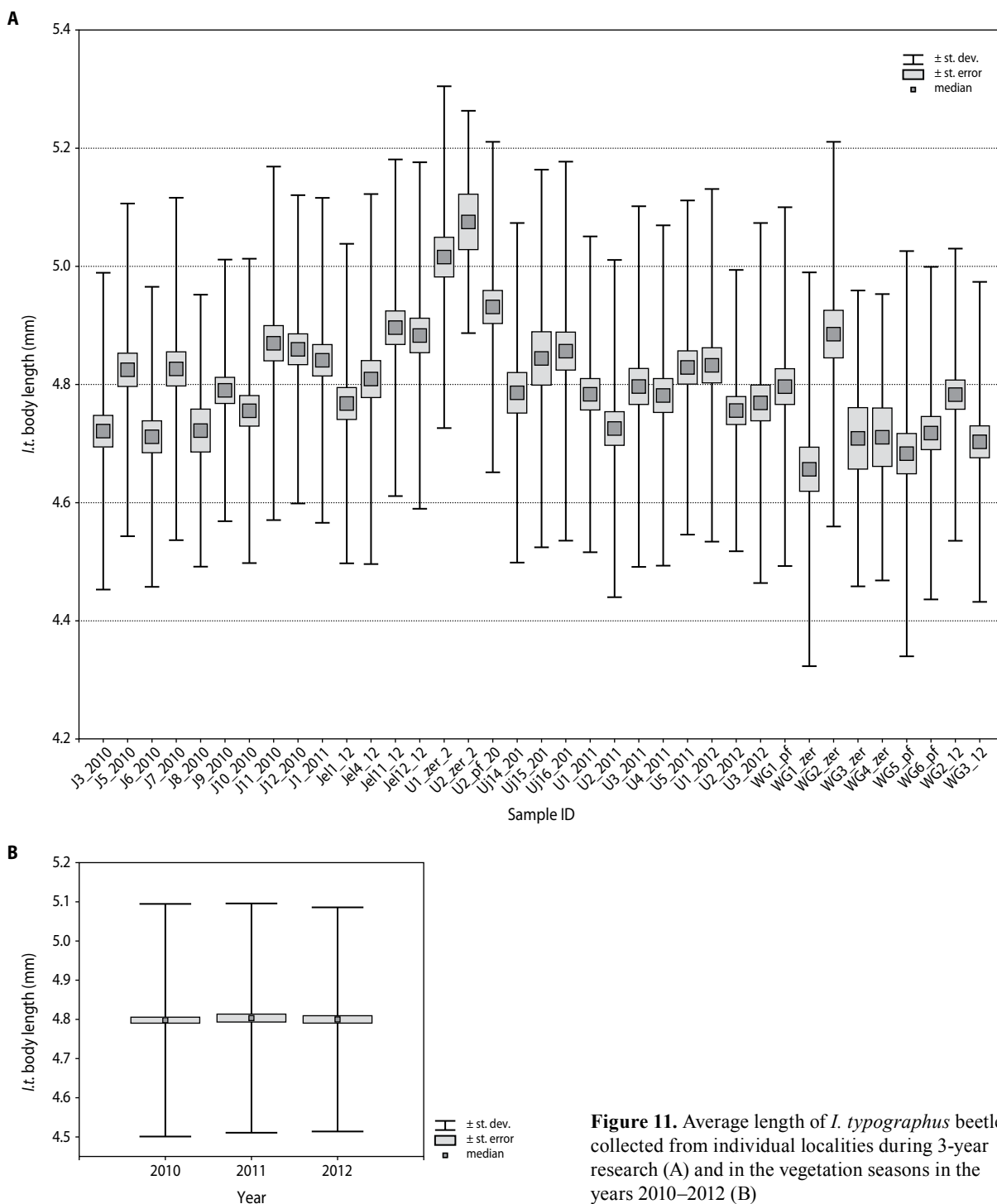


Figure 11. Average length of *I. typographus* beetles collected from individual localities during 3-year research (A) and in the vegetation seasons in the years 2010–2012 (B)

In two localities, it was possible to collect beetles from the galleries in the infested trees analyzed as well as from pheromone traps installed in close proximity. In the first locality (Ujsół) the beetles from the galleries

were significantly (ANOVA $F = 3.939$, $p < 0.05$) longer, while in the second one (Węgierska Górka) the pattern was opposite (longer beetles in pheromone traps) but this difference was not significant (fig. 14).

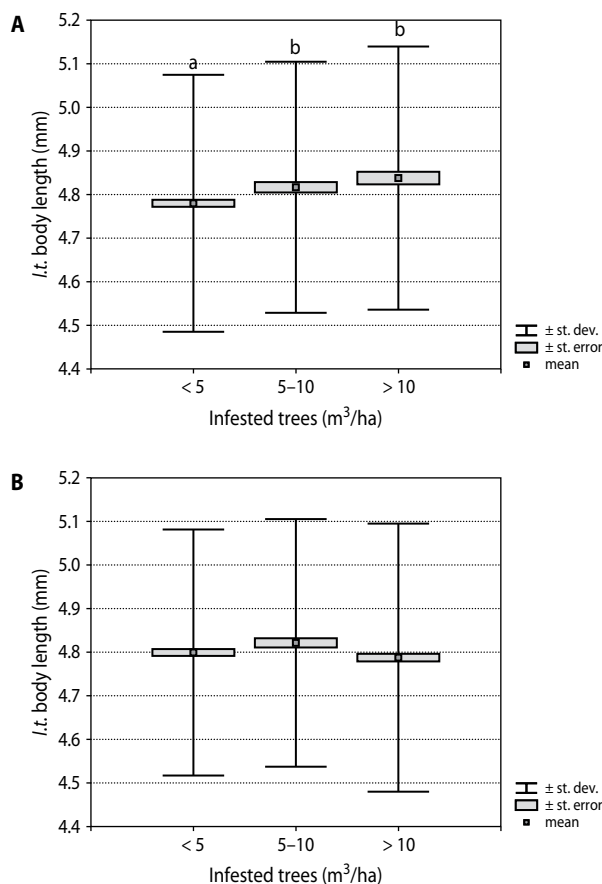


Figure 12. Average length of *I. typographus* beetles related to mortality of infested trees per 1 ha in the Beskid Żywiecki: in the year of beetle collection (A) and in the year before sampling (B)

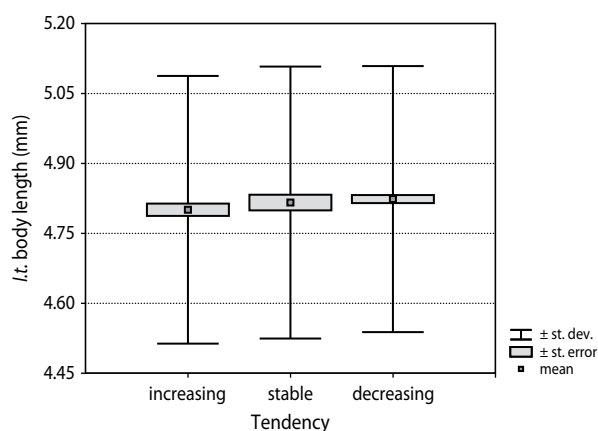


Figure 13. Average length of *I. typographus* beetles related to outbreak tendency determined for sub-compartments where *I. typographus* beetles were collected

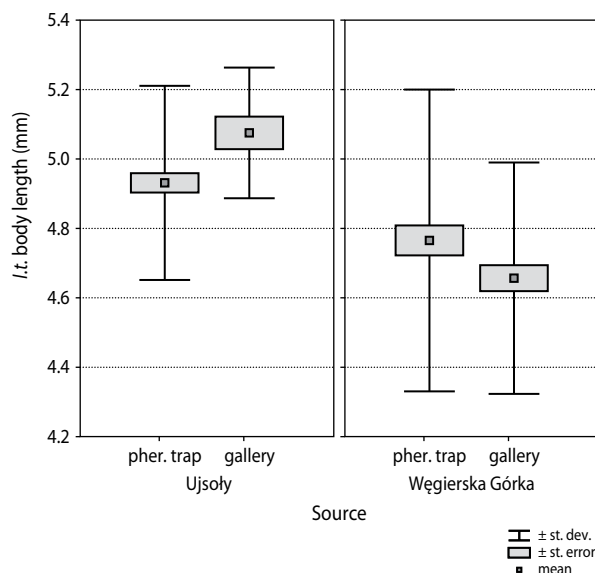


Figure 14. Average length of *I. typographus* beetles collected from galleries and pheromone traps at the same localities

DISCUSSION

The primary intention of the study was to explore spatial diversity of analyzed traits by defining sub-areas different in terms of outbreak phase. As the level of bark beetle-related tree mortality was highly variable within the study area (Grodzki *et al.* 2014), determination of such continuous sub-areas was not possible. Thus, we decided to analyze diversity of the traits in relation to some general features, regardless of spatial distribution of the study sites.

Infestation characteristics

The highest infestation density was found in the stands in which tree mortality due to bark beetle infestation (volume of infested trees) recorded in the year before the analysis was the highest, i.e. more than 10 m³/ha. In these stands, where *I. typographus* population density was already high, the attack of beetles on trees was very intense, which resulted in high infestation density. We can suppose that in line with the TSA model (Christiansen *et al.* 1987), very numerous beetles attacked relatively healthy trees, as it happens in outbreak eruptive phase or in the epidemic stage of bark beetle populations. The highest infestation density found in

the stands defined as being in the decreasing phase of the outbreak can indicate that bark beetle populations probably had to leave the infested stand due to very high population size, intraspecific competition and/or shortage in available breeding material (the effect of sanitary felling), and started to search for new infestation sites.

Distribution of gallery systems in relation to the number of maternal galleries was quite typical: the most frequent (38%) were the systems with 2 maternal galleries, although the systems with 1 and 3 galleries occurred frequently as well. Starzyk *et al.* (2000) also found prevalence (47.1%) of 2-gallery systems and high frequency of 1-gallery ones. Schlyter and Zhang (1995) pointed out that the harems with more than 2 females reduce female reproductive success due to larval competition. The pattern found in the Beskid Żywiecki should be seen as being related with species life strategy, ensuring high reproduction at an epidemic population level.

The average gallery length in our study material (6.75 cm) was lower than those reported from bark beetle outbreak area in the Šumava Mts. in the Czech Republic – 7.8 cm (Matoušek *et al.* 2012) and the Bieszczady Mts. in Poland – 7.4 cm (Starzyk *et al.* 2000). These differences may result from higher infestation density in the Šumava Mts. and the Bieszczady Mts. – 0.68 and 0.63 mating chamber/dm², respectively, versus 0.57 mating chamber/dm² in our study area, which can indicate lower tree resistance against the pressure of bark beetle populations in outbreak eruptive phase. On the other hand, density of maternal galleries per dm² observed in the present study – 1.05, as well as 1.15–1.23 reported by Starzyk *et al.* (2000) and – likely (taking into account infestation densities) in other studies mentioned above, was at least twice as high as 0.5 – the value reported as optimal for *I. typographus* reproduction (Schopf and Köhler 1995). Infestation density negatively affected the length of maternal galleries and oviposition, as it was earlier demonstrated by Anderbrant (1990) and Weslien (1994). Nevertheless, the diversity pattern of gallery length related to the harem size (the number of females in one gallery system), similar as this reported by Starzyk *et al.* (2000), confirms strong intraspecific competition mechanisms in *I. typographus*.

Based on laboratory tests, Anderbrant (1990) showed the relationship between the maternal gallery length and the number of eggs laid by the female, by means of the following regression equation:

$$y = 0.53x - 1.5$$

where: y is the number of eggs, x is gallery length.

If we applied this equation using our field data, the mean number of eggs in one maternal gallery would be 34.25, while the mean number calculated using our regression equation was 21.44 and the average value of observed data – 21.31. The possible reason of these differences might lay in environmental conditions: controlled in laboratory versus totally natural in the field, probably less favorable for oviposition and gallery construction on standing, living trees. It should also be noted, that our data concern “effective reproduction”, i.e. do not contain – contrarily to data reported by Anderbrant (1990) – laid eggs from which larvae did not emerge or died at early stages. Our results correspond with those reported by Lukášová *et al.* (2012) from another mountain area (Šumava, the Czech Republic), where the average number of eggs per female obtained from standing infested trees was 23.1. On the other hand, similar sampling done on lying trap trees (with weak or no defense mechanism) showed that the mean number of eggs laid by one female was 35 (Matoušek *et al.* 2012), thus it was higher than that in natural infestations of standing trees, which supports the hypothesis about the reasons of differences observed. The effect of infestation density (the number of gallery systems per a surface unit), determined as a factor slightly limiting both maternal gallery length and the number of progeny, reflects the mechanisms of intraspecific competition in *I. typographus*, known from several earlier studies (e.g. Anderbrant 1985; DeJong and Grijpma 1986).

Sex ratio

It was demonstrated that the sex ratio in *I. typographus* populations varied between outbreak phases – from 72% of females in progradation to about 50% in retrogradation (Lobinger 1996). All the same, a quite similar pattern seemed to appear in relation to bark beetle populations infesting windthrown trees in two outbreak areas in Poland: in the Gorce Mts. (Grodzki *et al.* 2006) and in the Tatra Mts. (Grodzki *et al.* 2007). When the outbreak reached its eruptive phase, the share of females increased – thus we supposed that the above rules should be valid also in relation to the populations attacking standing trees, and then useful for the assessment of outbreak tendency (Grodzki *et al.* 2011). Unfor-

tunately, it was not possible to demonstrate such pattern based on the results obtained in a relatively short time span (3 growing seasons) and from limited area. One of possible reasons could be the fact that the sex ratio is also variable within the growing season – more males occur during spring swarming when compared with later parts of the season (Faccoli and Buffo 2004), and the analyses were not performed always in the same part of the year. The material, represented by recently infested standing trees, was not available always and everywhere, so the choice of analyzed trees was – to a certain level – hazardous.

In case of *I. typographus* trees are attacked first by male beetles, then females are attracted to the nuptial chambers. According to the TSA model (Christiansen *et al.* 1987), successful infestation depends on the number of attacking beetles needed to overcome tree defense reaction at a given physiological and resistance status. This can explain higher number (and proportion) of males in the stands with higher tree mortality, where the number of attacking males is a driving factor. Faccoli and Buffo (2004), when analyzing seasonal variability of the sex ratio in *I. typographus* beetles caught in pheromone traps, demonstrated higher proportion of males during spring swarming than in other parts of the vegetation season. In multivoltine populations (observed in this study) the spring flight (and attack) is usually much more intense than in case of sister and second broods (Faccoli and Buffo 2004, Grodzki 2007). On the other hand, published results on the sex ratio in spruce bark beetle populations are hardly comparable with those obtained in the present study. The pattern of sex ratio variability during individual phases of an outbreak, described by Lobinger (1996), concerns *I. typographus* progeny in the galleries, while our results – the beetles attacking standing trees. The earlier findings (Grodzki *et al.* 2006, 2007) suggesting the similar pattern during infestation phase were based on beetles collected mostly from lying (broken or uprooted) trees, where weak or no defense mechanisms occur. Nevertheless, we have to conclude that – based on our results – the sex ratio of attacking beetles, especially generally increasing percentage of females during the 3-year study period, reflect high potential of observed *I. typographus* populations and point to their strong outbreak tendency in still ongoing epidemic phase in the Beskid Żywiecki.

Length of beetles

The results of measurements of body length of *I. typographus* beetles collected during 3 growing seasons did not statistically differ between the years of observation, thus it was decided to use pooled data for further analyzes. The longest beetles were collected in the stands with the highest tree mortality in the year of collection. Botterweg (1982) found that population density negatively influenced quality of individual beetles (expressed by elytra weight), however according to the TSA model (Christiansen *et al.* 1987) high tree mortality does not result directly from *I. typographus* population density, as attack density on trees can be similar in both epidemic and latent populations (Sallé *et al.* 2005). Thus, the variability in the length of beetles reflects rather quality of breeding conditions as a whole (including abundance of trees with reduced resistance). Consequently, in specific conditions (i.e. higher tree mortality) beetles were longer, which fits into the scheme proposed by Grodzki (2004). Larger length of beetles collected in the stands with decreasing tendency of tree mortality might result from shortages in exploited breeding material – the beetles from such “decreasing” sites spread to surrounding parts of stands with currently lower tree mortality. Such spreading of populations in tree stands could explain why the longest beetles were collected in the sites with medium level of tree mortality in the year before sampling.

There are some weak points concerning the sampling of beetles for body length measurement. The proposed pattern, found in relation to tree mortality in the current year only, suggests that the beetles collected for measurement originated from offspring generation captured in pheromone traps in late spring/early summer. The results obtained using overwintered beetles sampled in the spring would probably be different. The same concerns the question of local origin of sampled beetles, as the results concerning beetles collected from pheromone traps and from infested trees at the same localities are quite different, without any pattern. This could suggest that the beetles sampled from pheromone traps might not originate from local populations, as dispersal abilities in *I. typographus* are very high (Botterweg 1982, Gries 1985), consequently data from pheromone traps are relatively hard to use for the estimation of population spatial distribution (Grodzki 2007). Concluding, it seems that the size of beetles alone is still not a sufficient trait to predict population density trends (Sallé *et al.* 2005).

The present results were mainly obtained during field investigations (except for body measurements), therefore they are difficult to interpret. In field conditions it is not possible to keep the time regime when collecting data. As it was already mentioned, research materials (infested trees, beetles) are not available always and everywhere – it is *I. typographus* population which determines work timing and data quality in the last part. In view of this, experiments carried out in controlled (laboratory) conditions usually provide more homogenous data, thus much easier for statistical treatment. However, if we wish to study the traits or features of real populations or to validate the results from laboratory tests, the only way is to investigate populations in natural conditions, even though the patterns searched are more difficult to be found and confirmed.

Based on data on the volume of trees infested by bark beetles felled in forest sub-compartments, for the most part of the study area (Forest Districts Ujsoły and Węgierska Górka) outbreak phase was determined as retrogradation, and for the remaining area (Forest District Jeleśnia) as stabilization/latency (Grodzki *et al.* 2014). The traits analyzed in this study indicated high potential of bark beetle populations in terms of outbreak tendencies, suggesting that *I. typographus* was still in the epidemic stage within the whole investigated area. Taking into account the amount of potential breeding material offered by Norway spruce stands in this area and likelihood of wind or snow damage that stimulate bark beetle reproduction (Grodzki *et al.* 2006; Grodzki 2010), the risk of repeated outbreak in the Beskid Żywiecki should be assessed as extremely high.

CONCLUSIONS

- The analyzed traits of *I. typographus* showed high variability and dependence upon the local mortality of infested trees that indirectly reflects bark beetle population level, however the defined patterns of variability are not clear enough to enable their use as direct predictors of outbreak tendency in the future.
- These traits, however, indicate that *I. typographus* population in the study area represents very high outbreak potential, as the values obtained are typical for the populations at the epidemic stage or in progradation outbreak phase.
- This suggests that, in spite of decreasing volume of infested trees removed from Norway spruce stands in salvage cuttings during last years, bark beetle populations in the Beskid Żywiecki are still in eruptive phase and the risk of repeated outbreak in favorable weather/breeding conditions is extremely high.

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REFERENCES

- Anderbrant O. 1985. Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos*, 45, 89–98.
- Anderbrant O. 1990. Gallery construction and oviposition of the bark beetle *Ips typographus* (Coleoptera: Scolytidae) at different breeding densities. *Ecological Entomology*, 15, 1–8.
- Anderbrant O., Schlyter F. 1989. Causes and effects of individual quality in bark beetles. *Holarctic Ecology*, 12 (4), 488–493.
- Atkins M.D. 1975. On factors affecting the size, fat content and behaviour of a scolytid. *Zeitschrift für angewandte Entomologie*, 78, 209–218.
- Botterweg P.F. 1982. Dispersal and flight behaviour of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content. *Zeitschrift für angewandte Entomologie*, 94, 466–489.
- Botterweg P.F. 1983. The effect of attack density on size, fat content and emergence of the spruce bark beetle *Ips typographus* L. *Zeitschrift für angewandte Entomologie*, 96, 47–55.
- 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.

- DeJong M.C.M., Grijpma P. 1986. Competition between larvae of *Ips typographus*. *Entomologia Experimentalis et Applicata*, 41, 121–133.
- Faccoli M., Buffo E. 2004. Seasonal variability of sex-ratio in *Ips typographus* (L.) pheromone traps in a multivoltine population in the Southern Alps. *Journal of Pest Science*, 77, 123–129.
- Gries G. 1985. On the question of dispersal of the engraver beetle (*Ips typographus* L.) (in German with English summary). *Zeitschrift für angewandte Entomologie*, 99, 12–20.
- Grodzki W. 2004. Some reactions of *Ips typographus* (L.) (Col.: Scolytidae) to changing breeding conditions in a forest decline area in Sudeten Mountains, Poland. *Journal of Pest Science*, 77, 43–48.
- 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. 2010. The decline of Norway spruce *Picea abies* (L.) Karst. stands in Beskid Śląski and Żywiecki: theoretical concept and reality. *Beskydy*, 3 (1), 19–26.
- Grodzki W., Loch J., Armatys P. 2006. 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., Starzyk J.R., Kosibowicz M., Michalciewicz J., Mączka T. 2007. Effect of windthrows on the populations of cambio-phagous insects and threat to Norway spruce stands in the Tatra National Park. Report from the research done in 2004–2007 within the project 2 P06L 046 27 (in Polish). Instytut Badawczy Leśnictwa.
- Grodzki W., Starzyk J.R., Kosibowicz M. 2011. Can the functional traits in *Ips typographus* (L.) reflects its outbreak tendency? 80–85. *Freiburger Forstliche Forschung Berichte*, 89, 80–85.
- Grodzki W., Starzyk J.R., Kosibowicz M. 2014. Influence of selected stand characteristics on the intensity of bark beetle *Ips typographus* (L.) occurrence in Beskid Żywiecki (in Polish with English summary). *Leśne Prace Badawcze*, 2, 159–169.
- Lobinger G. 1996. Variations in sex ratio during an outbreak of *Ips typographus* (Coleoptera: Scolytidae) in Southern Bavaria. *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz*, 69, 51–53.
- Lukášová K., Holuša J., Grucmanová Š. 2012. Reproductive performance and natural antagonists of univoltine population of *Ips typographus* (Coleoptera, Curculionidae, Scolytinae) at epidemic level: a study from Šumava Mountains, Central Europe. *Beskydy*, 5 (2), 153–162.
- Matoušek P., Modlinger R., Holuša J., Turčáni M. 2012. Number of eggs laid by the spruce bark beetle *Ips typographus* (L.) (Coleoptera: Curculionidae: Scolytinae) on trap trees: influence of selected factors (in Czech with English summary). *Zprávy Lesnického Výzkumu*, 57 (2), 126–132.
- Netherer S., Nopp-Mayr U. 2005. Predisposition assessment systems (PAS) as supportive tools in forest management – rating of site and stand-related hazards of bark beetle infestation in the High Tatra Mountains as an example for system application and verification. *Forest Ecology and Management*, 207, 99–107.
- Sallé A., Baylac M., Lieutier F. 2005. Size and shape changes of *Ips typographus* L. (Coleoptera, Scolytinae) in relation to population level. *Agricultural and Forest Entomology*, 7, 297–306.
- Schlyter F., Zhang Q.-H. 1995. Testing avian polygyny hypotheses in insects: harem size distribution and female egg gallery spacing in *Ips* bark beetles. *Oikos*, 76, 57–69.
- Schopf R., Köhler U. 1995. Investigations on the population dynamics of spruce bark beetle in Bayerischer Wald National Park. In: Biberlriether, H. et al.: 25 years towards natural forest (in German). Passavia Druckerei GmbH, Passau, 88–109.
- Starzyk J.R., Graboń K., Hałdaś E. 2000. Cambio- and xylophagous insects in spruce (*Picea abies* (L.) Karst.) stands of the Upper San River Valley in the Bieszczady Mountain National Park (Eastern Carpathians). *Scientific Papers of the Agricultural University of Cracow, Forestry*, 29, 57–73.
- StatSoft, Inc. 2009. STATISTICA for Windows [Computer program manual]. Tulsa, OK: StatSoft, Inc., <http://www.statsoft.com>
- Weslien J. 1994. Interactions within and between species at different densities of the bark beetle *Ips typographus* and its predator *Thanasimus formicarius*. *Entomologia Experimentalis et Applicata*, 71, 133–143.