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ORIGINAL PAPER

Do *Ips typographus* (L.) beetles prefer the thickest trees? A retrospective study from Polish mountains

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ABSTRACT

It is generally believed that *Ips typographus* beetles prefer to infest and reproduce in trees with larger diameters. This preference has been documented at a stand level and on tree trunks lying on the ground, but much less is known about their preference of standing trees. The objective of the present study was to test the hypothesis that *I. typographus* shows a preference for the selection and infestation of thicker than average Norway spruce (*Picea abies*) trees in forest stands. For this purpose, past data collected by four independent research projects in Polish mountain areas were analysed. In the end, 15 plots with 1021 trees, of which 196 spruces were naturally infested during the surveys, were used for the analysis. Our results, collected during the progradation or retrogradation phases, did not confirm the hypothesised preferences. Only one out of the four research projects showed that mean diameter at breast height (DBH) was higher in infested than in non-infested trees, and in another project this pattern was found only at the plot level. The mean DBH of all the trees in the project confirming the hypothesis was the highest out of all four projects of concern. In that case, it is possible that preference at the stand level was the main driver of the 'general' pattern of *I. typographus* infestation. Finally, the results do not allow us to positively verify the tested hypothesis. The infested trees belonged mostly to the Kraft class 2 (codominant trees), *i.e.*, trees occupying a dominant proportion in the observed tree population. It appears that the position of the tree is much more important, as most colonised trees were at the stand edge. According to the TSA model, the main factors affecting infestation are bark beetle population density and individual tree resistance, which is a synergistic result of several factors related to both the tree itself and environmental conditions.

KEY WORDS

insect ecology, *Picea abies*, spruce bark beetle, stand characteristics, tree mortality

Introduction

The European spruce bark beetle, *Ips typographus* (L.) (Col.: Scolytinae), is one of the best-studied bark beetle species. Its biology and ecology have been well described (*e.g.*, Christiansen and Bakke, 1988; Skuhravý, 2002; Wermelinger, 2004; Grodzki, 2013). In *I. typographus*, the mechanisms of selecting trees to infest and colonise are well known (*e.g.*, Christiansen *et al.*, 1987; Christiansen and Bakke, 1988; Byers, 2004; Zhang and Schlyter, 2004), and so are the characteristics of stands that are susceptible to successful infestation by the beetles (*e.g.*, Netherer and

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Nopp-Mayr, 2005; Hilszczański *et al.*, 2006; Kamińska *et al.*, 2021). One such characteristic frequently mentioned by authors is the age of the tree. Reported ages can range from 70 to 100 years, depending on the author (*e.g.*, Becker and Schröter, 2000; Netherer and Nopp-Mayr, 2005; Grodzki *et al.*, 2014; Mezei *et al.*, 2014; Kamińska *et al.*, 2021). It is clear that, in most cases, the dimensions of trees (especially diameter at breast height, DBH) increase with the age of trees/stands. Therefore, according to published results, it is generally assumed that *I. typographus* beetles prefer to infest and reproduce in trees with a larger tree diameter (*e.g.*, Jakuš *et al.*, 2011; Sproull *et al.*, 2016). One limitation on tree size selection is also imposed by the minimum bark thickness required for beetle larval development (Grünwald, 1986). This is especially evident for wind-broken or fallen trees where large stems are more frequently infested (Göthlin *et al.*, 2000; Wermelinger, 2004), but it is not always true for standing trees when relationships are analysed using stand-level averages (Grodzki *et al.*, 2003; Lausch *et al.*, 2011). On the other hand, with respect to the dimensions of individual infested trees in the stand, little is known about the preferences of *I. typographus* beetles. Their preference for large trees is documented in several articles (*e.g.*, Schroeder *et al.*, 1999; Göthlin *et al.*, 2000), based on tree diameter (Schroeder, 2010; Abdullah, 2019) and basal area (Zolubas *et al.*, 2009; Sariyildiz and Duman, 2020). A positive relationship has been reported between tree DBH and *I. typographus* infestation (Schroeder *et al.*, 1999; Zolubas, 2006; Fettig *et al.*, 2007; Sariyildiz and Duman, 2020), but Lausch *et al.* (2011) found no significant differences in tree stand characteristics (tree DBH and increment) that could influence beetle preferences.

The objective of the present study was to test the hypothesis that *I. typographus* preferentially selects and infests thicker than average Norway spruce *Picea abies* (L.) H.Karst. trees in forest stands. For this purpose, past data collected during independent research projects in some Polish mountain areas were analysed.

Materials and methods

Data from four research projects were used for the analysis:

1. Western Sudety Mountains (later: Sudety) from 1992-1994. Stands studied after dramatic spruce decline, *I. typographus* populations were in the retrogradation phase (Capecki and Grodzki, 1998). A set of 17 plots of 25×50 m (54-100 trees) was established in the stands that survived the decline (Grodzki, 1998).
2. Tatra Mountains, eastern part (later: Tatry) from 2000-2001. Stands were studied after spruce decline; *I. typographus* populations were in the retrogradation phase (between two outbreaks) (Grodzki and Guzik, 2009). A set of 10 plots with 60 (active) or 30 (control) trees each (2×3 plots in the Polish and 2×2 plots in the Slovak part of the Tatra National Park) was established in the zone under active nature protection (Grodzki *et al.*, 2003).
3. The Gorce Mountains (later: Gorce) from 1999-2002. Stands were studied after spruce decline; *I. typographus* populations were in the retrogradation phase. A set of 12 plots of 100 trees each was established in the Gorce National Park and surrounding managed forests (Starzyk *et al.*, 2005).
4. Tatra Mountains, central part (later: Kośne Hamry) in 2018. Stands were studied after severe storm disaster and observations were made on surviving trees in the second growing season after wind damage; *I. typographus* populations were in the progradation phase. A set of 12 plots (6 in the active and 6 in the passive protection zone) with 20 trees each was operated (Grodzki and Gąsienica Fronek, 2019).

On each plot, trees were numbered, the diameter at breast height (DBH) was measured, and their biosocial status was assessed using Kraft classes (except for Kośne Hamry). During the survey period, plots were inspected at least twice in each growing season and trees infested by *I. typographus* were identified and recorded. Only plots where the number of infested trees reached at least 5% (Sudety) or 10% (other projects) were used for the analyses. The plots with 100% infested trees (Kośne Hamry, passive protection) were also excluded.

Finally, 15 plots with 1021 trees were used for the analysis, of which 196 spruce trees were successfully infested naturally (without additional attraction) by *I. typographus* during the surveys. Basic characteristics of the trees and stands are listed in Table 1. To facilitate access to additional information, the symbols of each plot are the same as in the corresponding references. The statistical data analysis (descriptive statistics, one-way ANOVA) was done using Statistica 13 (TIBCO, 2017) software.

Results

Sudety. A total of 321 trees were measured and observed in 4 plots, of which 31 were infested by *I. typographus* from 1992-1994. The mean (±SD) DBH of all trees was 22.8 ±5.0 cm, with the mean DBH of infested spruces being slightly lower (22.3 ±4.7 cm) than that of all trees and uninfested trees (22.9 ±5.0 cm). However, these differences were not significant (ANOVA F=0.403; p=0.526) and the pattern was not the same in the 4 individual plots. In 2 plots (nos. 3 and 7) the DBH of infested trees was lower than that of uninfested trees, in one plot (no. 8) the DBH was almost the same, and in only one plot (no. 5) the DBH of infested trees was higher (Fig. 1).

Tatry. A total of 120 trees were measured and observed in 2 plots, of which 34 were infested by *I. typographus* from 2000-2001. The mean DBH of all trees was 36.9 ±8.2 cm, with the mean

Table 1.

Basic characteristics of the observation plots in four study areas in Polish mountains (symbols of plots same as in the corresponding references)

Plot no.	Location (Forest sub-district or national park, forest compartment	Altitude a.s.l. [m]	Stand age [years]	Number of trees observed	DBH ±SD [cm]	Infested trees [%]
			Sudety*			
3	Świeradów, 428b	900	85	54	22.7 ±5.7	20
5	Piechowice, 101a	800	60	100	21.1 ±4.2	9
7	Świeradów, 214c	620	65	92	25.1 ±5.0	5
8	Szklarska Poręba, 161g	860	80	75	22.6 ±4.4	8
			Tatry**			
A	Tatra National Park, 70a	1300	135	60	36.6 ±8.5	33
E	Tatra National Park, 65l	1100	125	60	37.1 ±7.9	27
			Gorce***			
B	Nowy Targ, 103b	950	80	100	32.0 ±7.2	16
C	Nowy Targ, 103b	950	80	100	33.9 ±7.8	18
G	Gorce National Park, 117b	1100	85	100	26.5 ±7.6	24
H	Gorce National Park, 111c	1000	90	100	33.8 ±10.5	12
L	Gorce National Park, 127b	1100	85	100	34.2 ±6.8	21
			Kośne Hamry****			
2	Tatra National Park, 39a	950	100-160	20	29.5 ±5.8	80
3	Tatra National Park, 36a	1000	90	20	30.6 ±6.4	70
4	Tatra National Park, 37a	1000	80-100	20	35.1 ±5.1	15
5	Tatra National Park, 17l	1050	100	20	37.3 ±6.1	20

* Grodzki, 1998; **Grodzki *et al.*, 2003; *** Starzyk *et al.*, 2005; **** Grodzki and Gąsienica Fronek, 2019

DBH of infested spruces being higher (37.3 ±8.6 cm) than that of all trees and uninfested trees (36.7 ±8.0 cm). These differences were not significant (ANOVA F=0.112; *p*=0.738) and this pattern was not identical in the individual plots. In one plot (plot A), the DBH of infested trees was lower than that of uninfested trees, while in another plot (plot E) it was reversed (Fig. 2).

Gorce. A total of 500 trees were measured and observed in 5 plots, of which 91 were infested by *I. typographus* from 1999-2002. The mean DBH of all trees was 32.1 ±8.6 cm, with the mean DBH of infested spruces (30.2 ±9.8 cm) being lower than that of all trees and uninfested trees (32.5 ±8.2 cm). In this case, the differences were significant (ANOVA F=5.247; *p*=0.022). The pattern where the DBH of infested trees was lower than that of uninfested ones was similar in 4 out of 5 plots (plots B, C, G and L), while it was the opposite in only one plot (plot H) (Fig. 3).

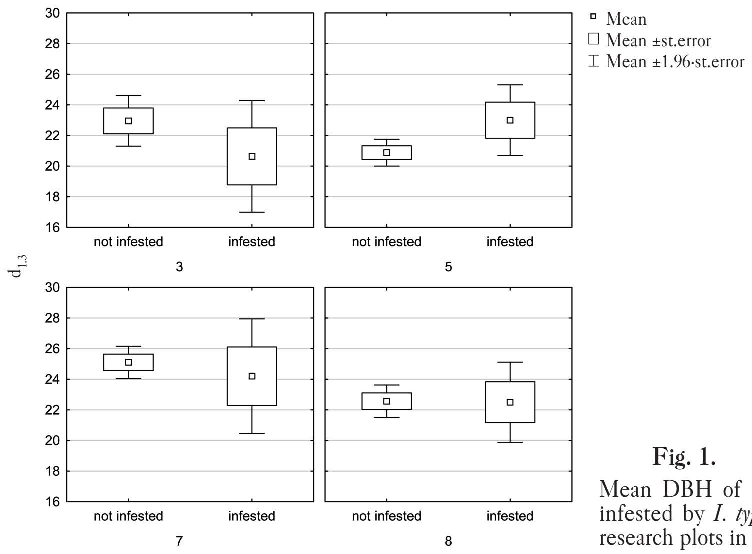

Fig. 1.
Mean DBH of trees infested and not infested by *I. typographus* in individual research plots in Sudety from 1992-1994

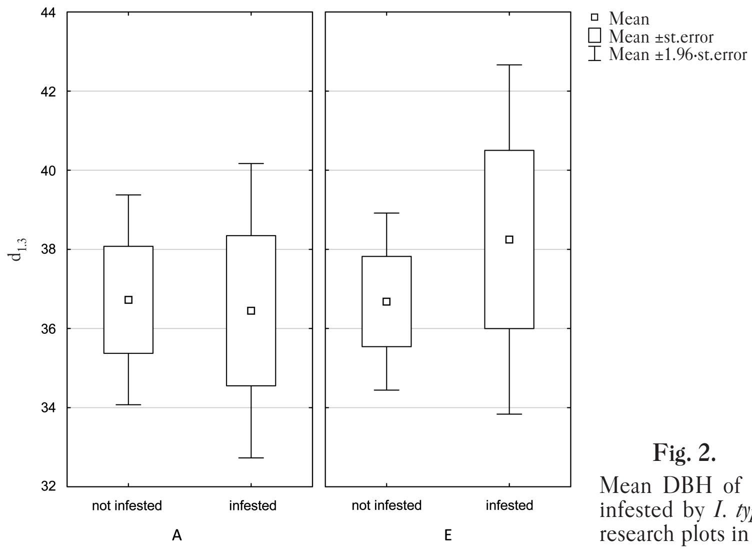

Fig. 2.
Mean DBH of trees infested and not infested by *I. typographus* in individual research plots in Tatry from 2000-2001

Kośne Hamry. A total of 80 trees were measured and observed in 4 plots, of which 43 were infested by *I. typographus* in 2018. The mean DBH of all trees was 33.1 ±6.6 cm, with the mean DBH of infested spruces (32.0 ±5.7 cm) being lower than that of all and uninfested trees (34.1 ±7.2 cm). However, these differences were not significant (ANOVA F=2.002; *p*=0.161). At the individual plot level, the DBH of infested spruce trees was higher than uninfested trees in 3 of the 4 plots, and no difference was seen in plot 4 (Fig. 4).

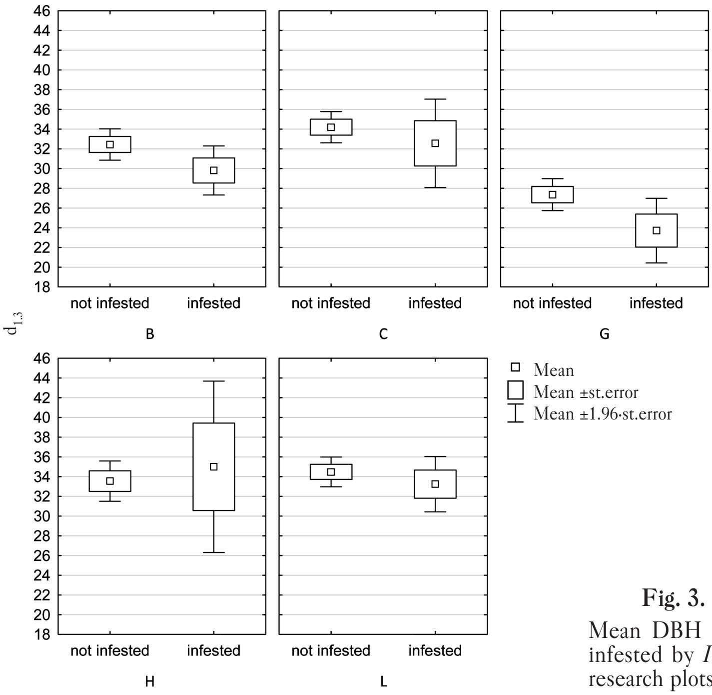

Fig. 3.

Mean DBH of trees infested and not infested by *I. typographus* in individual research plots in Gorce from 1999-2002

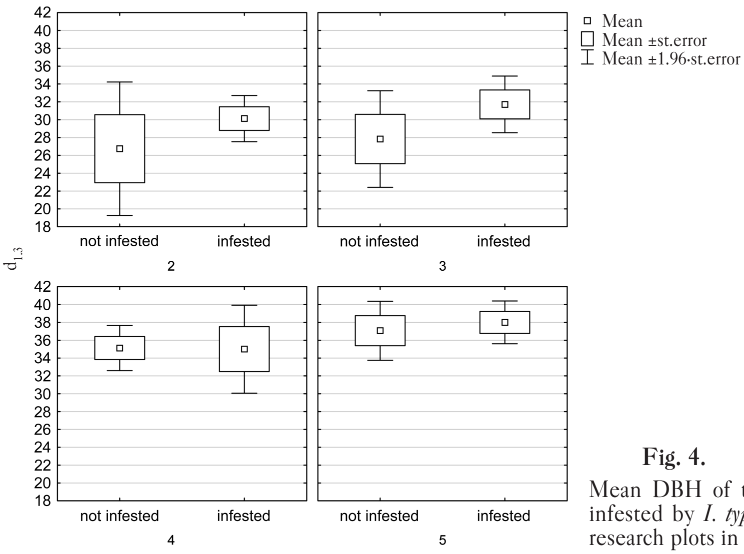

Fig. 4.

Mean DBH of trees infested and not infested by *I. typographus* in individual research plots in Kośne Hamry in 2018

Biosocial status of infested trees. In all four projects, the sample of infested spruces were predominately codominant trees (Kraft class 2): in Sudety it made up 45% of the populations, in Tatry it was 56%, and in Gorce the proportion was 40%. The percentage of dominant trees was the highest in the Tatry project (19%) and very low in the Sudety project (6%) (Fig. 5).

Discussion

It is generally accepted that *I. typographus* infestations tend to occur in older stands (Netherer and Nopp-Mayr, 2005; Grodzki *et al.*, 2014) where trees are larger, as indicated by a higher DBH or basal area (Hilszczański *et al.*, 2006; Jakuš *et al.*, 2011). Higher growing stock of the stand, related to larger tree size, is thought to increase the likelihood of successful bark beetle infestation – and subsequent tree mortality (Negrón *et al.*, 2009; Zolubas *et al.*, 2009). This pattern applies more generally, as it is also valid for *I. typographus* infestations of *Picea orientalis* (L.) Link (Sariyildiz and Duman, 2020), *Dendroctonus pseudotsugae* Hopkins infestations of Douglas fir *Pseudotsuga menziesii* (Mirb.) Franco (Fettig *et al.*, 2007), and *Dendroctonus rufipennis* (Kirby) infestations of Engelmann spruce *Picea engelmanii* Parry ex Engelm. (Schmid and Frye, 1976). However, the above references focussed on large trees that shaped the overall stand, rather than preferences for individual trees.

Preference for larger trees is well documented in freshly fallen stems in wind-damaged stands. Here, larger diameter trees are more susceptible to colonization by bark beetles (*e.g.*, Wermelinger, 2004; Borkowski, 2011; Lausch *et al.*, 2011). Bark beetle preference of thicker trees (standing and lying on the ground) may be a result of the minimum bark thickness required for complete larval development (Grünwald, 1986; Lausch *et al.*, 2011).

For individual trees, the preferences of *I. typographus* with respect to tree DBH are much less well-known. In the study described by Zolubas (2006), infested trees were larger than healthy trees. Schroeder (2010) reported a positive relationship between DBH and the colonization probability of artificial high stumps, and emphasized the preference of *I. typographus* for large diameter trees (see also Butovitsch, 1971; Schroeder *et al.*, 1999; Göthlin *et al.*, 2000). In the Eriksson *et al.* (2005) study, the minimum diameter of sample trees was 10 cm compared to the 15 cm reported by Schroeder (2010).

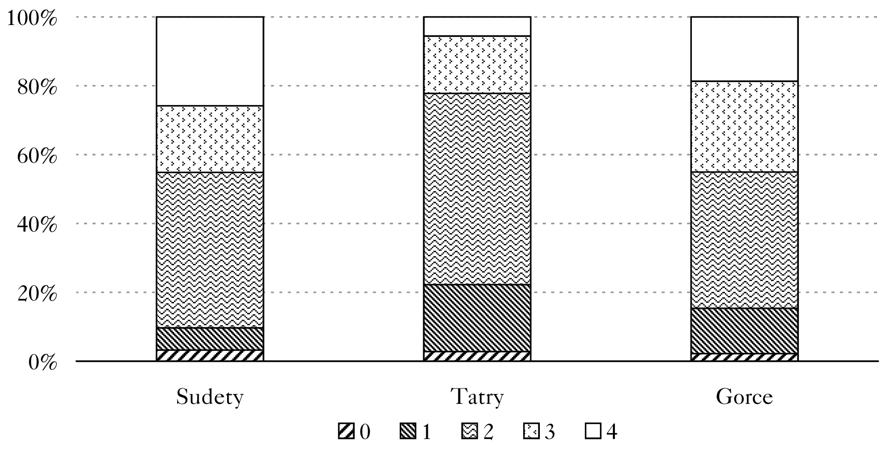

Fig. 5.

The distribution of infested trees in Kraft classes in the plots in Sudety, Tatry and Gorce
0 – individual trees, 1 – dominant, 2 – codominant, 3 – intermediate, 4 – suppressed trees

The results from the Norway spruce stands in the protected areas of the Tatras showed that the preferences of *I. typographus* with respect to tree DBH were not stable in the individual outbreak phases. In the progradation and retrogradation phases, the larger trees were selected more frequently. In the culmination phase, trees with a broader range of stem diameters were infested, *i.e.*, tree size was not as important (Sproull *et al.*, 2015). The 2013 survey of wind-damaged stands conducted in the Kościeliska Valley (Tatras) showed that along with the development of the outbreak *I. typographus* colonised larger trees, which required higher attack intensity (Grodzki and Gąsienica Fronek, 2018). Data from another protected area in Poland (Babia Góra) also suggest that larger trees were more frequently selected for infestation at later stages of the outbreak (*i.e.*, retrogradation) (Sproull *et al.*, 2016). In the eastern part of Tatras in Poland, measurements of standing trees that survived wind damage showed that spruce trees infested by *I. typographus* were thinner than uninfested trees in the first stage (progradation), while the pattern was reversed in the next stage (Grodzki and Gąsienica Fronek, 2018). Our analysis was focussed on the data collected during the progradation or retrogradation phase, but no such clear preferences were found. Out of the four projects, only one (Tatry) showed the mean DBH to be higher in infested than in uninfested trees. In another project (Kośne Hamry) this pattern was found only at the plot level. The mean DBH of all trees in the Tatry project was the highest among all four objects of concern. In this case, it is possible that preference at the stand level was the main driver of the 'general' pattern of *I. typographus* infestation. Finally, our results do not allow us to positively verify the tested hypothesis.

According to the TSA model (Christiansen *et al.*, 1987), *I. typographus* preferred the weaker (thinner) trees in the first phase. Only later, after reaching the required population level in the stands that were not subjected to control measures (Grodzki and Gąsienica Fronek, 2018), the stronger (thicker) trees were selected. On the other hand, Horntvedt (1988) found no correlation between tree DBH and resistance to bark beetle attack.

The infested trees mostly belonged to the 2nd Kraft class (codominant trees), *i.e.*, trees with a dominant proportion in the observed tree population. These results are consistent with data reported by Zolubas (2006) and suggest that biosocial position may be of secondary importance. The position of the tree at the stand edge appears to be much more important, which is where most colonized trees were located. This 'sun effect' is considered a crucial factor that increases local infestation probability at recent forest edges (Kautz *et al.*, 2013).

As population density increases, the tree dimension preference of *I. typographus* decreases. According to the TSA model, the main factors affecting tree infestation are bark beetle population density and individual tree resistance. The latter is a synergistic effect of several factors related to both the tree itself and environmental conditions.

Conflicts of interest

The author declares no conflict of interest.

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STRESZCZENIE

Czy chrząszcze *Ips typographus* (L.) preferują najgrubsze drzewa? Retrospektywne studium z polskich gór

Kornik drukarz *Ips typographus* (L.) należy do najlepiej zbadanych gatunków korników – dotyczy to zwłaszcza stopnia poznania mechanizmów rządzących wyborem przez chrząszcze drzewa do zasiedlenia. Powszechnie uważa się, że kornik preferuje drzewostany starsze, w których w znacznym udziale występują drzewa o znacznych rozmiarach, wyrażonych wielkością pierśnicy bądź pierśnicowego pola przekroju. Skłonność *I. typographus* do zasiedlania grubych drzew została udokumentowana na poziomie drzewostanowym, a także w odniesieniu do drzew powalonych przez wiatr. Znacznie mniej wiadomo o jego preferencjach w stosunku do pojedynczych drzew stojących wybieranych do zasiedlenia. Celem niniejszej pracy było przetestowanie hipotezy zakładającej, że kornik drukarz wybiera drzewa grubsze niż przeciętne w drzewostanie. W tym celu wykorzystano dane zebrane w ramach projektów badawczych zrealizowanych w kilku rejonach polskich gór. Dane te, wybrane na podstawie przyjętych kryteriów (występowanie co najmniej 5 lub 10% drzew zasiedlonych w obserwowanej populacji świerków), pochodziły z badań w następujących obiektach: Sudety Zachodnie (dalej: Sudety) lata 1992-1994 – 4 z 17 powierzchni; wschodnia część Tatr (dalej: Tatry) lata 2000-2001 – 2 z 10 powierzchni; Gorce lata 1999-2002 – 5 z 12 powierzchni; Tatry – Kośne Hamry (dalej: Kośne Hamry) 2018 r. – 4 z 12 powierzchni (tab. 1). Na każdej powierzchni drzewa zostały oznaczone numerami i pomierzono ich pierśnice, a także (z wyjątkiem obiektu Kośne Hamry) określono ich stanowisko biosocjalne. W okresie prowadzenia badań co najmniej dwa razy w roku rejestrowano występowanie drzew zasiedlonych przez kornika drukarza. Wykorzystane w pracy dane pochodziły z 1021 drzew na 15 powierzchniach, spośród których 196 zostało w okresie obserwacji zasiedlonych w sposób naturalny przez kornika drukarza. W obiekcie Sudety średnia (±odch. stand.) pierśnica drzew zasiedlonych (22,3 ±4,7 cm) była nieco niższa niż wszystkich drzew (22,8 ±5,0 cm) oraz drzew niezasiedlonych (22,9 ±5,0 cm), przy czym wzorzec ten nie dotyczył powierzchni rozpatrywanych indywidualnie (ryc. 1). W obiekcie Tatry średnia pierśnica drzew zasiedlonych (37,3 ±8,6 cm) była nieco wyższa niż wszystkich drzew (36,9 ±8,2 cm) oraz drzew niezasiedlonych (36,7 ±8,0 cm), przy czym wzorzec ten był odmienny na poszczególnych powierzchniach (ryc. 2). W obiekcie Gorce średnia pierśnica drzew zasiedlonych (30,2 ±9,8 cm) była nieco niższa niż wszystkich drzew (32,1 ±8,6 cm) oraz drzew niezasiedlonych (32,5 ±8,2 cm), przy czym wzorzec ten był zachowany na 4 z 5 powierzchni (ryc. 3). W obiekcie Kośne Hamry średnia pierśnica drzew zasiedlonych (32,0 ±5,7 cm) była niższa niż wszystkich drzew (33,1 ±6,6 cm) oraz drzew niezasiedlonych (34,1 ±7,2 cm), przy czym na poziomie poszczególnych powierzchni wzorzec był odwrotny (ryc. 4). W trzech obiektach objętych oceną wśród drzew zasiedlonych przeważały te z II klasy Krafta (współpanujące), natomiast najwyższy udział górujących drzew zasiedlonych stwierdzono w obiekcie Tatry (ryc. 5).

Istniejące w literaturze informacje dotyczące skłonności kornika drukarza do zasiedlania grubszych lub najgrubszych drzew w drzewostanie są skąpe i niejednoznaczne. Podkreślana jest także zmiana jego preferencji w tym zakresie w kolejnych fazach gradacji. Przedstawione w niniejszej pracy dane, zebrane w fazach pro- i retrogradacji, nie pozwalają na pozytywne zweryfikowanie postawionej hipotezy, a wyniki mogące ją potwierdzać dotyczą drzewostanów o wyższej średniej pierśnicy, co może wskazywać na istotniejszą rolę preferencji na poziomie drzewostanowym niż w skali pojedynczych drzew. Preferencje kornika drukarza co do grubości zasiedlanych drzew zmniejszają się w miarę wzrostu liczebności jego populacji. Ostatecznie jednak, zgodnie

z modelem TSA, o wyborze drzew do zasiedlenia decyduje, oprócz liczebności populacji kornika, ich indywidualna odporność, będąca wypadkową cech samego drzewa oraz czynników środowiskowych.