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ORIGINAL ARTICLE

The occurrence of bark beetles on cut Norway spruce branches left in managed stands relative to the foliage and bark area of the branch

Magdalena Kacprzyk · Bartłomiej Bednarz

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Abstract This study addresses the relationships between the foliage and bark area of Norway spruce (*Picea abies*) branches left in the forest after managing large timber: the densities of infestation by *Pityogenes chalcographus*, *Pityophthorus pityographus* and *Dryocoetes autographus*; and the reproductive efficiency of *P. chalcographus*. Based on the models developed in this study, a positive correlation was found between the foliage area of spruce branches and the densities infested by *P. chalcographus* and *D. autographus*, though a higher negative correlation was found in relation to the size of the branch bark area (BA) and the infestation densities. A negative correlation for the branch BA was also found on *P. pityographus*. This result shows that the desiccation of branches affects the infestation densities of bark beetles. In contrast, the size of the branch BA was positively correlated with the reproductive efficiency of *P. chalcographus*, with higher reproductive efficiency on the branches from the outer layer of the pile than on disorderly scattered branches on the ground.

Keywords Branch desiccation · *Dryocoetes autographus* · Infestation density · *Pityogenes chalcographus* · *Pityophthorus pityographus*

Introduction

Climate conditions, i.e. temperature and humidity, are particularly important in the infestation and reproduction processes of cambiophagous and xylophagous insects (Harding et al. 1986; Lobinger 1994; Wermelinger and Seifert 1998). Moreover, the diversity of environmental conditions associated with variable temperature and humidity affects not only the insects themselves but also the physiological state of the material constituting the feeding and breeding base for phloemophagous species (Grünwald 1986; Bouget and Duelli 2004). On the one hand, insect-favouring microclimate conditions are correlated with increased temperatures and promote phloem and xylem changes that enable infestation by beetles. On the other hand, high temperatures and water lost from breeding material may prevent the further development of insects (Grünwald 1986; Jakuš 1995; Martikainen et al. 1996; Peltonen and Heliövaara 1999; Sauvard 2004; Kula and Kajfosz 2006). The biochemical changes occurring in felled or broken trees confirm this argument because decomposition proceeds more rapidly in fallen or broken trees, and these trees are the first to be infested by insects. In contrast, wind-fallen trees are not inhabited by cambio- and xylophagous insects until the second year after injury due to their vitality, which is sustained by a partly functional root system (Inouye 1963; Schroeder and Eidmann 1993; Göthlin et al. 2000). Indeed, the connection between the tree and its root system is one of the most important factors in determining the physiological state of the tree with regard to the degree of decomposition and the tree's resistance to bark beetle infestation (Kataev et al. 1984; Jakuš 1995). Moreover, the breeding material from the spring–summer season becomes "available" for insects due to immediate biochemical changes that occur in the phloem; in contrast, the material from the autumn–winter period undergoes these processes much more slowly while increasing with time elapsed since the tree injury (Führer 1981). Such observations are the basis for classic traps in

M. Kacprzyk (✉) · B. Bednarz
Department of Forest Protection, Entomology and Forest Climatology, University of Agriculture in Kraków, 31-425 Al. 29 Listopada 46, Kraków, Poland
e-mail: m.kacprzyk@ur.krakow.pl

the form of branchless trees, a common practice in forest protection during the autumn–winter period. Leaving felled trees with an assimilation apparatus for a few months causes intensive water loss, which, in turn, affects the attractiveness of the material for insects when swarming begins. It may be assumed that this attractiveness also applies to branches or treetops cut from trunks that, similar to felled trees, provide an attractive breeding base for bark beetles. Therefore, the disposal method and placement of logging residue in the manipulation area may play a crucial role in the process of colonisation by insects (Röker 1986; Göthlin et al. 2000). The importance of branch utilisation methods relative to the *Pityogenes chalcographus* infestation intensity and its breeding success was recently described by Kacprzyk (2012) for weakened Norway spruce (*Picea abies*) stands in southern Poland. It was shown that branches left at the forest operating area after incidental cutting and scattered in a disorderly manner were statistically more densely infested by *P. chalcographus* than were those collected in piles. The opposite significant relationship was found for species reproductive efficiency (Kacprzyk 2012). However, the relationship between how the phloem of logging residue is modified by different treatments and the feeding dependence of various spruce bark beetle species on this phloem have not been examined. The present study proposes the hypothesis that the size of the foliage and bark area of spruce branches left in the forest after logging operations has a direct impact on the attractiveness of this material to bark beetles. The aim of this study is to determine the effects of foliage and bark area of the branches in the context of differing methods of branch utilisation (in piles or scattered disorderly on the ground) on infestation intensities and the reproductive efficiency of bark beetles on Norway spruce branches.

Materials and methods

Study sites and establishment of the experiment

The research was conducted in 2006 in 3 sites located in the Żywiec Beskids, southern Poland (Jeleśnia Forest District, Korbielów Forest Division—49°34′08.15″N, 19°19′55.08″E; Sucha Forest District, Mosorne Forest Division—49°39′14.25″N, 19°33′20.48″E; Nowy Targ Forest District, Stańcowa Forest Division—49°29′35.26″N, 19°37′20.22″E). The study sites were located in 75- to 120-year-old Norway spruce (*Picea abies*) stands that were growing at an elevation of 875–1,100 m.a.s.l. in mountain mixed fir and spruce forest habitats (*Abieti-Piceetum montanum* and *Galio-Piceetum*) (Table 1). The stands were characterised with a condition of reduced health expressed as the percentage of the insect-infested timber volume to the total timber volume harvested from the stand at 0.34–0.68 % (Table 1). Fresh spruce branches left as logging residue in the forest no longer than 1 week after tree felling and debranching at each study site in early spring (Korbielów—15 April, Stańcowa—26 March, and Mosorne—10 April) were used in this study. The branches were documented by digital photography using a Canon EOS 450D digital camera with a CMOS sensor (resolution of 12.2 megapixels) that was equipped with a standard Canon lens (focal length of 18–55 mm and light 1:3.5–5.6). A randomly selected branch was placed on a white 5.0 × 1.5 m sheet with a grid of 10.0-cm squares. Photographic documentation of the branch was performed at constant lens parameters using a tripod setup such that the camera matrix was parallel to the plane of the photographed branch. The branch length was measured from the place of the cut to the distal end of the branch, and the diameter of the thicker end of the branch was also measured. The foliage area (FA) of the branch was determined as a two-dimensional projection using SigmaScan Pro 5.0 (for Windows 98) software. To eliminate the geometric distortion of the image, each photographed branch was calibrated by setting the coordinates of three points on a square grid of known dimensions, which acted as a background for the horizontal projection of the branch. The calibrated images were converted to an 8-bit digital greyscale map, and the branch transpiration area was determined. The size of the foliage branch area was calculated to an accuracy of 100 cm^2. The branch bark area (BA) was determined based on the field measurements of the branch parameters using the equation for conical surface, and the values had an

Table 1 Characteristics of the study sites

Forest district	Study site	Altitude (m.a.s.l.)	Potential plant community	Age	Stand volume (m^3 ha^{-1})	Canopy cover[a]	ITVI (%)[b]
Jeleśnia	Korbielów	1,100	*Abieti-Piceetum montanum*	122	282	0.4	0.68
Sucha	Mosorne	1,050	*Abieti-Piceetum montanum*	115	563	1.1	0.34
Nowy Targ	Stańcowa	875	*Galio-Piceetum*	75	412	1.0	0.58

[a] The proportion of the tree canopy surface projection to the stand surface. The index is described as 1.0 when tree canopies cover whole stand surface and in case that tree canopies covering whole stand surface overlap each other, the index is over 1.0

[b] The proportion of mean insect-infested timber volume to the volume of all timber within the period of 1999–2005

accuracy of 50 cm^2. The photographed and measured branches were piled as stacks or scattered randomly in plots in each stand for <1 week after felling and debranching to prepare the branches prior to bark beetle swarming, i.e. in the first half of April. The presented methods of branch management are the most common disposal method practiced in forest protection in Europe. The branch piles and plots with randomly scattered branches were located in open spaces where the stand density was intermittent. The piles were approximately 1.40–1.60 m high, with a base diameter ranging 2.20–2.50 m. The minimum distance between the piles was 10 m and that between the plots was 30 m. A plot area was 0.01 ha (10 m square), and the number of branches used in a single plot ranged from 80 to 100. The same number of branches was used to create one pile. Branches not used in the experiment were removed from the study sites. A total of 20 spruce-branch piles and 10 plots were arranged at each study site.

Infestation density analysis

Entomological analyses of the branches were performed four times; that is, every 2 weeks from the first half of July to the second half of August 2006. The branch colonisation intensities by the most numerous cambiophagous species, i.e. *P. chalcographus*, *Pityophthorus pityographus*, *Dryocoetes autographus*, *Ips amitinus*, *Cryphalus abietis* and *Hylurgops palliatus*, were determined. Five branches from the outer layer (i.e. ~30 cm within the pile) of each of 18 piles of all 60 piles and 5 branches in each of 18 plots of all 30 plots were randomly selected. Thus, 90 infested branches from the piles and 90 infested branches that had been randomly scattered (i.e. each variant of branch utilisation: Korbielów $n = 30$; Mosorne $n = 35$; Stańcowa $n = 25$) were analysed. From all of the analysed branches, 41 originated from the first half of July (i.e. Korbielów $n = 15$; Mosorne $n = 14$; Stańcowa $n = 12$), 44 from the second half of July (i.e. Korbielów $n = 17$; Mosorne $n = 15$; Stańcowa $n = 12$), 44 from the first half of August (i.e. Korbielów $n = 18$; Mosorne $n = 14$; Stańcowa $n = 12$), and 51 from the second half of August (i.e. Korbielów $n = 20$; Mosorne $n = 17$; Stańcowa $n = 14$). The branches from the outer layer of the pile were selected due to the possibility of free evaporation from the foliage and woody surface of the branches, similar to the loosely scattered material that was exposed to the drying process. At each sampling, a new branch was used for entomological analysis. In order to keep the piles and plots with branches randomly scattered in their established state, each examined branch was returned to its original location. The branch infestation density ID was calculated as the sum of nuptial chambers and mother galleries of each bark beetle species per 100 cm^2 of bark area in the second half of August.

Reproductive efficiency analysis

The bark beetle reproductive efficiency was estimated in September and October in the laboratory using 50-cm branch fragments, sampled at 50 cm from their base, of 5 branches from the piles or plots at the Korbielów ($n = 40$) and Stańcowa ($n = 60$) study sites. Due to the lack of numerous branch infestations by bark beetles at Mosorne, the material from this site was not used for the entomological analysis. The technique used for the analysis and the calculation of reproductive efficiency index (IRE) was based on the methods proposed by Kacprzyk (2012). The IRE was defined as the total number of progeny beetles per total number of parent individuals colonising the branch. To calculate the reproductive efficiency, all holes (entrance, exit, or ventilation) in the analysed branch section were punctured with a metal skewer prior to debarking. The reproductive efficiency was determined only in relation to *P. chalcographus*, as the most common bark beetle species in the analysed branches. The galleries of *P. chalcographus* were distinguished from the galleries of other species by the shape and size of the mother galleries (Kacprzyk 2012). The areas marked during branch debarking included nuptial chambers, mother galleries, and ventilation holes established by the parent *P. chalcographus* individuals and exit holes made by the offspring. It was assumed that each offspring individual made one exit hole.

Modelling assumptions

A linear regression analysis for the infestation density and reproductive efficiency indices was performed using qualitative explanatory variables: study site, variants of branch arrangement (variant1, pile; variant2, randomly scattered), date of inspection (date1, first half of July; date2, second half of July; date3, first half of August; date4, second half of August), and continuous explanatory variables (the foliage area and bark area of the branch). To clarify the functions of the developed models, the branch infestation density by each insect species was described using the ID abbreviation, and the IRE value was adopted for the reproductive efficiency of *P. chalcographus*. When matching the regression functions with the variables of infestation density and reproductive efficiency, zero values were omitted due to both the uneven distribution between the study sites and the inability to reach the assumptions of normality and independence of the residues. For the index of branch infestation by *P. chalcographus*, *P. pityographus* and *D. autographus*, such cases occurred for 21, 64 and 86 datapoints, respectively, and 24 datapoints for the reproductive efficiency of *P. chalcographus*. The optimal set of independent variables describing the variation in the infestation density of each of the described species and the reproductive efficiency of *P. chalcographus* were selected using the Akaike criterion. Instability of the variance was observed in each of the cases and resulted from differences between the analysed study sites. Therefore, the dependent variables were transformed to obtain stability in the residual variance. Furthermore, all the independent variables were transformed to log $(x + 1)$ to eliminate skewed distributions; these transformed data are labelled with the addition of the value "1" to the beginning of the ID. The variables "date2", "date3" and "date4" were equal to "1", "2" and "3", respectively, whereas the variable "date1" was equal to "0". Constant variance for the IRE was achieved by modifying the IRE variable depending on the value of the branch treatment method variable. Statistical analyses were performed using R software v.2.2.1. (R Development Core Team 2005).

Results

The analysed spruce branches were characterised by different parameters within each study site. The mean foliage area was 2- and 3-fold higher in the Korbielów and Stańcowa areas, respectively, compared to the mean bark area (Table 2). The foliage and bark area of branches showed similar values in the Mosorne study site (Table 2). The entomological analyses showed six bark beetle species infesting the spruce branches, with *P. chalcographus* being the most common (Table 3). In respect to all sampling period dates, the infestation density of *P. chalcographus* ranged from 2.9 individuals per 100 cm^2 at the Mosorne study site to 17.5 individuals per 100 cm^2 at the Korbielów and Stańcowa study sites. Similar values were obtained for the second half of August for branches originating from Korbielów and Mosorne. For the Stańcowa study site, the ID index obtained for entire period investigated was higher by ~ 3 individuals per cm^2 than in the second half of August. *P. pityographus* and *D. autographus* were the most numerous insects among the remaining species (Table 3). Models applied to the infestation densities for these three dominant species at three study sites are indicated in Table 4. In the models referring to *P. chalcographus* (Eq. 1a, c in Table 4), variables contributed to 97 % of the variability in the branch infestation density (adjusted *R*-squared value = 0.9703, *F* statistic = 600.4 on 8, $df = 144$, $P < 0.001$), whereas the variables contributed to 87 % of the variability in the case of *D. autographus* (Eq. 3a–c in Table 4) (adjusted *R*-squared value = 0.871, *F* statistic = 74.4 on 8, $df = 79$, $P < 0.001$). A significant influence on the branch density infestation by *P. chalcographus* was found for two of the three included model predictors, i.e. date2 ($a_2 = -0.20766$; $P = 0.012$) and BA ($a_4 = -0.24035$; $P = 0.015$) (Tables 4, 5). Similar predictors were confirmed as significant also in the case of *D. autographus*, and the FA variable included also had a statistically significant influence on ID ($a_3 = 0.19258$; $P < 0.001$) (Tables 4, 5). The positive coefficients for FA for these two species indicate that the infestation density increased proportionally with foliage area. In contrast, the negative coefficient for BA indicates that the beetles were significantly more numerous on branches with a smaller bark area (Tables 4, 5). In the model referring to *P. pityographus* (Eq. 2a–c in Table 4), variables contributed to 83 % of the variability in the infestation density (adjusted *R*-squared value = 0.8355, *F* statistic = 111.8 on 5, $df = 104$, $P < 0.001$). For the regression describing the relationship between the *P. pityographus* infestation density on the analysed branches, three predictors, i.e. variant1 ($a_2 = 2.7521$; $P < 0.001$), variant2 ($a_3 = 2.4149$; $P < 0.001$), and BA ($a_4 = -0.7410$; $P < 0.001$), were found to be significant in the developed model (Tables 4, 5). The negative coefficient for BA indicates that *P. pityographus* was significantly more numerous on branches with smaller bark area. The larger coefficient for variant1 than for variant2 indicates that the branches collected from the outer layer of the pile were more infested with *P. pityographus* than were the randomly scattered branches (Tables 4, 5). The linear regression models (Eq. 4a, 4b described below) describing the *P. chalcographus* reproductive efficiency was based only on the BA variable and was confirmed as statistically significant. The calculated parameters of the model determining 81 % of the reproductive efficiency of *P. chalcographus* on the branches sampled from the outer pile layer (Eq. 4a) and on the branches randomly scattered throughout the plot (Eq. 4b)

Table 2 Parameters (foliage area and bark area) of the Norway spruce (*Picea abies*) branches used in the analyses of infestation density and reproductive efficiency of bark beetles

Study site	No. of branches	Foliage area (100 cm^2)			Bark area (100 cm^2)		
		Mean	SE	Min.–max.	Mean	SE	Min.–max.
Korbielów	100	19.06	1.15	0.99–73.30	9.14	0.52	2.93–31.40
Mosorne	70	8.26	0.43	2.76–21.66	8.22	0.32	3.01–15.21
Stańcowa	110	20.32	1.11	3.16–64.40	6.93	0.35	2.46–20.43

Table 3 Infestation rates (%) expressed as the number of infested branches by each bark beetle to the total number of analysed branches on the all sampling periods and the second half of August

Species	Study site		
	Korbielów $N = 60^a/n = 20^b$	Mosorne $N = 70/n = 17$	Stańcowa $N = 50/n = 14$
Pityogenes chalcographus	100 (17.5)/100 (16.1)	70.4 (2.9)/64.7 (2.7)	100 (17.5)/100 (14.4)
Pityophthorus pityographus	60.0 (2.4)/50.0 (3.2)	85.9 (7.0)/76.5 (10.9)	28.6 (1.2)/21.4 (1.2)
Dryocoetes autographus	63.3 (1.1)/45.0 (0.6)	29.6 (0.6)/23.5 (1.1)	66.7 (2.6)/35.7 (2.9)
Ips amitinus	53.3/55.0	4.2/5.9	–
Cryphalus abietis	25.0/10.0	–	19.3/14.3
Hylurgops palliatus	4.2/4.2	–	–

The numbers in parentheses indicate the average infestation densities per 100 cm^2 of bark area of the three dominant species

[a] *N* the total number of infested analysed branches

[b] *n* The number of infested branches analysed at the second half of August

Table 4 Empirical equations describing the density of Norway spruce branch infestation by the tree dominant bark beetle species for different study sites

Species	Study site	Equation (code)
P. chalcographus	Korbielów	$\log(\mathrm{ID}+1) = a_1 + a_2\cdot\mathrm{date2} + a_3\cdot\mathrm{FA} + a_4\cdot\mathrm{BA}$ (1a)
	Mosorne	$\log(\mathrm{ID}+1) = b_1 + a_2\cdot\mathrm{date2} + a_3\cdot\mathrm{FA} + a_4\cdot\mathrm{BA}$ (1b)
	Stańcowa	$\mathrm{ID}^{0.3} = c_1 + a_2\cdot\mathrm{date2} + a_3\cdot\mathrm{FA} + a_4\cdot\mathrm{BA}$ (1c)
P. pityographus	Korbielów	$\log(\mathrm{ID}+1) = a_2\cdot\mathrm{variant1} + a_3\cdot\mathrm{variant2} + a_4\cdot\mathrm{BA}$ (2a)
	Mosorne	$(\log(\mathrm{ID}+1))^{0.8} = b_1 + a_2\cdot\mathrm{variant1} + a_3\cdot\mathrm{variant2} + a_4\cdot\mathrm{BA}$ (2b)
	Stańcowa	$\mathrm{ID}^{1.5} = c_1 + a_2\cdot\mathrm{variant1} + a_3\cdot\mathrm{variant2} + a_4\cdot\mathrm{BA}$ (2c)
D. autographus	Korbielów	$\log(\mathrm{ID}+1) = a_1 + a_2\cdot\mathrm{date4} + a_3\cdot\mathrm{FA} + a_4\cdot\mathrm{BA}$ (3a)
	Mosorne	$\mathrm{ID} = b_1 + a_2\cdot\mathrm{date4} + a_3\cdot\mathrm{FA} + a_4\cdot\mathrm{BA}$ (3b)
	Stańcowa	$(\log(\mathrm{ID}+1))^{0.3} = c_1 + a_2\cdot\mathrm{date4} + a_3\cdot\mathrm{FA} + a_4\cdot\mathrm{BA}$ (3c)

ID infestation density (number of nuptial chambers and egg galleries per 100 cm^2 of bark area); *date2* second half of June; *date4* second half of August; *variant1* pile; *variant2* scattered; *FA* foliage area of the branch; *BA* bark area of the branch; a_1, a_2, a_3, a_4, b_1, c_1 equation parameters

showed an increase in the IRE index with increasing BA, because of the significant and positive value of a_1 ($a_1 = 0.60909$, $P < 0.001$) (adjusted R-squared value = 0.813, F statistic = 340.1 on 1, $df = 77$, $P < 0.001$). This result indicates that *P. chalcographus* achieved a higher reproductive efficiency for the branches with a larger bark area.

$$\sqrt{\mathrm{IRE}} = a_1 \cdot \mathrm{BA} \quad (4a)$$

$$\mathrm{IRE} = a_1 \cdot \mathrm{BA} \quad (4b)$$

At Stańcowa, reproductive efficiency of *P. chalcographus* was significantly higher on branches on piles than on those scattered in plots (Table 6).

Discussion

Optimal bark beetle development relies on microhabitat conditions, the amount of available food, and breeding material and shelter (Blake and Hoppes 1986; Harding et al. 1986; Bouget and Duelli 2004). In addition, the microsuccession of bark beetles infesting trees also depends on the state of the insect population. Weakened defenceless trees, such as windthrows, windbreaks, and logging residues, are the most attractive breeding material for colonisation by bark beetles (Nilsson et al. 2001). Although felled trees may be inhabited over long periods due to their attractiveness (Wermelinger 2002), the material classified as logging residue may rapidly lose its attractiveness. The material available for cambio- and xylophagous insects is largely determined by the rate of biochemical changes occurring in the phloem. The variables of temperature and humidity play a key role in this process (Bouget and Duelli 2004), and the temperature, ambient humidity, and water content of the material also have a direct impact on insects, particularly during the early stages of their development (Wermelinger and Seifert 1998). Thus, in addition to the thermal and moisture conditions, the breeding success of the investigated group of bark beetles depends to a large

Table 5 Parameters and basic statistics of equations for the determination of *P. chalcographus*, *P. pityographus*, and *D. autographus* density infestation index on Norway spruce branches

Species	Parameters of equation		SE	*t* value	*P* value
P. chalcographus	a_1	3.10366	0.23515	13.198	0.0000
	b_1	1.62024	0.21672	7.476	0.0000
	c_1	2.47771	0.24006	10.321	0.0000
	a_2	−0.20766	0.08146	−2.549	0.0118
	a_3	0.12926	0.07129	1.813	0.0719
	a_4	−0.24035	0.09802	−2.452	0.0154
P. pityographus	b_1	0.5534	0.1348	4.104	0.0000
	c_1	0.4634	0.2142	2.164	0.0328
	a_2	2.7521	0.4212	6.534	0.0000
	a_3	2.4149	0.4290	5.630	0.0000
	a_4	−0.7410	0.1972	−3.758	0.0003
D. autographus	a_1	0.89127	0.25253	3.529	0.0007
	b_1	0.78126	0.25184	3.102	0.0027
	c_1	1.07214	0.25602	4.188	0.0000
	a_2	0.64963	0.17533	3.705	0.0004
	a_3	0.19258	0.07298	2.639	0.0100
	a_4	−0.36355	0.09931	−3.661	0.0004

extent on the physiological state of the material. The material exposed to direct solar radiation appears to be more attractive for infestation by insects due to a stronger release of volatile attractants (Bouget and Duelli 2004), even though, as reported by Ehnström (2001), bark beetles appearing on spruce generally prefer shaded places. Therefore, it must be concluded that the selection of the material to be colonised by cambio- and xylophagous insects is strictly related to the rate of desiccation, which is particularly important in the case of logging residue because this type of material cannot replace water sustainably. Needled branches left in an open space show increased transpiration (Morén et al. 2000). It has been reported that material exposed to long-term intensive solar radiation was colonised by six-toothed bark beetles (Röker 1986). As the reduction of the assimilation apparatus decreases transpiration, the size of the foliage area of branches left in the forest after tree debranching may be closely linked to the water-loss rate, thus enabling determination of its variable quality. The results obtained in this study demonstrate a positive correlation between the transpiration area of spruce branches and the infestation density of *P. chalcographus* and *D. autographus*; however, the bark area negatively affected the branch infestation their density (Tables 4, 5). Although the presence of *P. chalcographus* on variously dried branches is indisputable due to the high ecological plasticity of this species, the lack of a negative correlation between the infestation density and both variants of branch arrangement and their foliage area with respect to *D. autographus*, which is the most demanding species regarding the physiological state of the phloem (Schroeder et al. 1999; Kula et al. 2011), was a surprising result. An occurrence of *D. autographus* in thinner, less foliaged areas of surface branches left in stands after logging operations may be partially due to the unique pluvial and thermal conditions prevailing during the growing season in the year of the study (Durło 2007). The lack of precipitation with simultaneous high temperatures in spring and the beginning of summer may have caused relatively rapid water loss from the needled branches. Therefore, it is most likely that this material would have become the most convenient breeding base due to its infestation in early spring. From the perspective of species' ecological preferences, the fact that *D. autographus* swarming occurs approximately 1 month after the swarming of the other analysed spruce bark beetles (Rudinsky 1962) could have been the underlying cause for this species inhabiting only the most weakened branches that showed the smallest foliage area. In contrast, an interesting relationship was found in terms of the impact of the foliage area and bark area on the reproductive efficiency of *P. chalcographus*. The limiting effect of the foliage area on breeding success was not confirmed, whereas a positive correlation with the bark area was observed. Furthermore, the increase in BA caused a higher reproductive efficiency for the infested branches originating from the outer layer of the pile than the randomly scattered branches (Table 6). The breeding success of cambiophagous insects is related to the type of the material available, particularly the bark thickness, which is one of the most important elements limiting the selection of material for occupation (Price 1997). It is assumed that the larger and thicker branches, with a relatively larger feeding and breeding base (phloem thickness) and increased water content in comparison to

Table 6 Reproductive efficiency of *P. chalcographus* expressed as the total number of progeny per total number of parent individuals

Study site	Outer layer of the pile				Randomly scattered				Result of Mann–Whitney *U* test	
	n[a]	Mean	SE	Min.–max.	n	Mean	SE	Min.–max.	U	P
Korbielów	20	2.05	0.33	0.48–5.84	20	1.43	0.21	0.24–4.22	150.0	0.1806
Stańcowa	17	2.52	0.42	0.06–5.76	21	1.27	0.11	0.43–2.11	78.0	0.0345

[a] Number of analysed branch fragments colonised by *P. chalcographus*

smaller and thinner branches, were capable of providing better conditions for the development of the progeny of *P. chalcographus*. In parallel, the reduced infestation of thicker branches with larger foliage areas could have reduced the intraspecific competition among the species discussed, thus having a significant impact on the breeding efficiency of *P. chalcographus*. The results obtained in this study reject the initial hypothesis: bark beetles were frequent in strongly degraded spruce stands and infested the available breeding material as rapidly as possible, thereby filling the available ecological niches. Therefore, material desiccation becomes a secondary factor. Following the rapid loss of needles, without the possibility of supplemental water, and with the assimilation apparatus exposed to direct sunlight, spruce branches attract beetles (particularly in the initial swarming period) in direct proportion to their area but do not impact the infestation density. It may also be presumed that the period during which the branch is exposed to environmental factors plays a significant role in bark beetle infestation, i.e. the density may be inversely proportional to the time of exposure. The attractiveness of branches devoid of needles varies with their thickness and determines the reproductive success of *P. chalcographus*. In contrast, branches with larger bark areas may have a relatively higher water supply and, therefore, may be more convenient material for the development of *P. chalcographus* progeny. In contrast, small branches that dry much more quickly, though allowing massive bark beetle infestation, do not allow the production of a new bark beetle generation.

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