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Preference−performance relationship and influence of plant relatedness on host use by *Pityogenes chalcographus* L.

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Abstract
1 *Pityogenes chalcographus* L. (Coleoptera: Scolytinae) causes damage in European coniferous forests, primarily on *Picea abies* L. Karst., but is also recorded on other native and exotic Pinaceae species. Estimating the adequacy between adult preference and larval performance of this beetle among its host-range, as well as the influence of plant taxonomic relatedness on these parameters, would provide useful information on the beetle's ability to shift onto novel hosts.
2 Choice and no-choice assays were conducted under laboratory conditions. Adult preference and larval performance parameters among two native (*Pinus sylvestris* L. and *Picea abies*) and three exotic north American [*Pinus contorta* Dougl., *Picea sitchensis* (Bong.) Carr. and *Pseudotsuga menziesii* Mirbel (Franco)] conifer species were measured.
3 *Pityogenes chalcographus* exhibited a significant positive relationship between preference and performance. *Picea abies* was both the preferred and the most suitable host species for larval development. The closest relative, *P. sitchensis*, was the second best choice in terms of preference and performance. *Pseudotsuga menziesii* occupied an intermediate position for both beetle preference and performance, and *Pinus* spp. were the least suitable hosts for beetle development.
4 Adult preference and larval performance ranking among hosts provides little support to the plant taxonomic relatedness hypothesis. Taxonomic relatedness could play a role on the diet breadth, although only at a limited scale, within the genus *Picea*. At higher taxonomic levels, other factors such as bark thickness might be decisive.

Keywords Bark beetle, exotic, native, performance, Pinaceae, *Pityogenes chalcographus* (Coleoptera: Scolytinae), preference, resource similarity, taxonomic relatedness.

Introduction

The increase in global travel and trade favours the dispersal of organisms and modifies their geographical range, thus creating new interactions. Phytophagous insects, for example, are increasingly confronted with novel hosts, either within their natural range as a result of plant introductions or in new geographical areas where insects are introduced. These new interactions can result in extensive insect damage that threatens natural and agricultural ecosystems (Strong, 1974a, b; Liebhold

et al., 1995). In this context, knowledge of adult preference and larval performance of insect pests among actual and potential host plants is of particular importance and has both an economical and ecological interest. Both traits can affect the insects' potential host range and their ability to shift onto novel, exotic hosts. To colonize a new host, or for a successful host shift to occur, an insect should be able to recognize it and accept it as a valuable substratum for oviposition, and larvae should be able to develop on the host (Agosta, 2006). When a novel plant is both among the preferred species of an insect pest and a suitable substratum for its larval development, significant damage is likely to occur. Many theoretical and empirical studies on phytophagous insects have examined the prediction that female oviposition preferences will be positively correlated

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with larval performance. However, these studies have yielded results, ranging from good to poor correlation (Jaenike, 1990; Thompson & Pellmyr, 1991; Mayhew, 1997; Gratton & Welter, 1998; Agosta, 2006). According to the phylogenetic constraint hypothesis (Price, 1994; Craig & Ohgushi, 2002), a good match between oviposition preference and larval performance requires two conditions. First, insects should lay their eggs within plant tissues, where, during host tissue penetration, they will be able to detect cues related to host suitability for larval development. Second, larval development should depend on oviposition site, which will generate a selective pressure on adult oviposition preference.

Several factors can modulate adult preference and larval performance among potential hosts. The presence of native congeners appears to ensure better colonization on exotic tree species by indigenous phytophagous insects (Connor *et al*., 1980; Lieutier, 2006; Roques *et al*., 2006), suggesting that taxonomic relatedness could influence host plant selection. In some cases, however, the likelihood to shift on a novel host is related to resources similarities among plants rather than to phylogenetic relatedness (Ehrlich & Raven, 1964; Becerra, 1997; Wahlberg, 2001). However, because related plants tend to exhibit high chemical and morphological similarities, the effect of taxonomic relatedness or resources similarities are often difficult to distinguish.

Bark beetles (Coleoptera: Scolytinae) are the most important pests in conifer forests in the world (Grégoire & Evans, 2004). Although tree killing bark beetle species have a host range mainly restricted to a particular tree genus (Sauvard, 2004), many have been observed on a wide variety of hosts in the wild, on which larval development has been demonstrated under laboratory conditions (Chararas, 1973; Wainhouse & Beech-Garwood, 1994). Thus, scolytids exhibit a certain level of plasticity in both their host selection behaviour and larval development, allowing them to attack exotic trees, often among congeners of their usual host (Sauvard, 2004), suggesting an influence of plant taxonomic relatedness.

Pityogenes chalcographus (L.) occasionally attacks stands of young spruce (Chararas, 1962) and is sometimes regarded as a serious pest in European spruce forests (Grégoire & Evans, 2004). *Pityogenes chalcographus* primarily develops in *Picea abies* L. Karst., but has also been recorded in other native and exotic Pinaceae species. Members of the genera *Picea*, *Larix*, *Pinus*, *Abies* and *Pseudotsuga* can serve as alternative hosts (Chararas, 1962; Pfeffer, 1994). Similar to other bark beetle species, host selection is performed by dispersing males, probably through visual or olfactory signals from the host tree (Byers, 2004; Campbell & Borden, 2006). Once they have selected a host, males emit aggregation pheromones that attract both sexes, and excavate a nuptial chamber in the phloem. Each male is joined by three to nine females, each of which excavates an egg gallery in the phloem where it oviposits in niches (Klauser, 1954). Larval development, pupation and adult maturation all take place in the phloem, after which adults emerge from the tree (Chararas, 1962). Three phases of the life cycle can potentially be influenced by the host tree: host selection, oviposition behaviour and brood development. According to the phylogenetic constraints hypothesis (Price, 1994; Craig & Ohgushi, 2002), and because

parents are in contact with oviposition site prior to laying eggs and larvae are forced to develop at the oviposition site, a positive correlation among these parameters would be expected. Estimating the adequacy among host selection, oviposition behaviour and brood development could give information on the beetle's ability to damage introduced hosts and would help in building effective monitoring and control methods in European multispecific conifer forests, where planting of exotic tree species has increased in many regions. It would also provide knowledge on the status of *P. chalcographus* as an exotic pest in the non-Palaearctic countries, where it may be introduced.

The present study aimed to estimate the adult preference and larval performance of *P. chalcographus* among several Pinaceae species. According to the optimal oviposition and phylogenetic constraint hypotheses (Jaenike, 1990; Craig & Ohgushi, 2002), we hypothesized that these parameters would be positively correlated. The first objective was to determine the variation of adult preference and larval performance among different Pinaceae species. We also hypothesized that preference and performance would be affected by plant taxonomic relatedness. The second objective was to test whether or not the preference–performance ranking was related to host phylogeny. Choice and no-choice assays were performed with logs from five native or exotic Pinaceae species within the beetle's host range.

Materials and methods

Biological materials

Adults of *P. chalcographus* were collected from *P. abies* trap-trees located in two forests of the Limousin region in France: Chamboux (45°40′N, 002°00′E) and Larfeuil (45°30′N, 001°57′E). The trees were felled in February 2007 and colonized by beetles during spring. In May, the trees were cut into 1-m long logs, brought to the laboratory, and placed at 20°C in plywood boxes (124 × 35 × 65 cm) equipped with collector tubes. Adults emerged the second and the third week of June 2007. Beetles were sexed according to the elytral declivity pattern (Pfeffer, 1994) and placed at 4°C (1–2 days) until used in experiments.

To test the influence of taxonomic relatedness on adult preference and larval performance, two pairs of native and exotic congeneric host species were used: *Pinus sylvestris* L. versus *Pinus contorta* Dougl., and *P. abies* versus *Picea sitchensis* (Bong.) Carr. *Pseudotsuga menziesii* Mirbel (Franco), which has no congener in Europe, was also used for comparison. *Pinus sylvestris*, *P. contorta* and *P. menziesii* originated from INRA plantations (Orléans, France), and *P. abies* and *P. sitchensis* originated from the Chamboux forest. Two to three trees per species were harvested during the first week of June 2007, cut into logs of similar size and brought to the laboratory. For all tree species, log length, diameter and bark surface were 25.05 ± 0.12 cm, 11.85 ± 0.18 cm and 90.0 ± 2.0 cm^2 (mean $\pm$ SE), respectively. Bark thickness was measured with callipers at two points at each end of the log. To prevent logs from degradation and drying, they were stored at 4°C after each extremity had been sealed with paraffin. Logs were used within

2 weeks after felling, and were warmed at room temperate 1 day before starting the experiments.

Choice assays

During the third and the last week of June 2007, 14 containers (height: 78 cm, lower and upper diameter: 51 and 71 cm, respectively) were filled with five logs (one of each tree species) placed randomly in a vertical position, leaving free the central zone of the containers. Twenty adults (five males and 15 females) were randomly chosen and placed on the bottom in the centre of each container. Containers with the insects were left outdoors, covered with tulle and protected from rain. A control container was set up with five logs of *P. abies*. Ninety-six hours later, each log was isolated in a tulle bag, brought to the laboratory and kept under long day conditions (LD 16:8 h) at $24 \pm 2 °C$. Two months later, bark was removed and the number of entrance and exit holes, number of nuptial chambers, number and length of fertile egg galleries (with egg niches), number of egg niches, larval galleries and emerging adults were recorded. Elytra length (mean between right and left) and pronotum width were measured on a maximum of 30 emerging adults per log, under a dissection microscope (Motic®, China) coupled with a camera (Motic Image Plus®). Images were analysed with the ImageJ (version 1.32j) software (NIH, Bethesda, Maryland). All measurements were made at × 40 magnification by the same investigator.

No-choice assay

Two successive generations of *P. chalcographus* were studied during the second and the third week of June 2007. Ten logs originating from two or three trees of each Pinaceae species were each drilled through the bark to the cambium level, with one hole (1.5 mm in diameter) near each log end. One male *P. chalcographus* was introduced into each hole, followed 24 h later by one female. Holes were covered with a plastic capsule to prevent beetles from escaping. Each log was placed vertically into a box covered with tulle and kept under the same laboratory conditions as in the choice assays, to allow the first generation of *P. chalcographus* to develop. Two months later, two logs of the same species containing the first generation were placed into a container with two or three new logs belonging to the same tree species, so that emerging insects were allowed to attack new logs and produce a second generation brood. Six to ten such replicates were performed per tree species. This experiment allowed us to evaluate whether the larval host affected host acceptance and brood performance. Two months later, the bark was removed from all logs and the same parameters as for choice assay were recorded for both generations.

Statistical analysis

All variables were checked for their homoscedasticity (Levene test) and normal distribution (Shapiro–Wilk test). Non-normal data were $\log(x + 1)$ or ArcSin$\sqrt{x}$ transformed. Data that did not fit a normal distribution after transformation were analysed with nonparametrical tests.

Adult preference. Beetle preference among hosts was assessed with attack density (i.e. density of entrance holes per dm^2). Whether beetles accepted or rejected their host after contact was estimated with two parameters: nuptial chambers and egg galleries.

For the choice assay, densities of attack, nuptial chambers (with and without egg galleries) and fertile egg galleries (with egg niches) were estimated. Linear models were used to measure adult preference, and host species were ranked according to the model coefficient. In our assays, both fixed (host species) and random (container) effects may affect adult preference. In our linear models, fixed effects affect the mean of the response variable, whereas random effects affect the variance (Pinheiro & Bates, 2002). To avoid misleading interpretation of results because of random effects, we used mixed effects linear models that consider both the fixed effect and random deviations around this effect (i.e. random effect) (Pinheiro & Bates, 2002). Three models, corresponding to three response variables (densities of attack, nuptial chambers and fertile egg galleries) were built with host species as explanatory variable. The only random effect was container, and we also checked that it had no significant fixed component (for a similar procedure concerning the spatial variation of Taylor's power law, see Certain *et al.*, 2007).

A Kruskal–Wallis test was performed to assess whether bark thickness differed among species and Spearman's correlation coefficient (r_s) were calculated to check for relationships between bark thickness and adult preference parameters.

For the no-choice assay, numbers of fertile nuptial chambers (with egg galleries) and fertile egg galleries were recorded for the first generation. The effect of tree species on these parameters was investigated with a Kruskal–Wallis test. For the second generation, to test the ability of beetles to develop successive generations on the same host, we considered the same parameters as in the choice assay. However, because the number of emerging beetles from the first generation differed among host species, ratios were calculated. For each host species, we considered the ratios of attack, nuptial chambers and fertile egg galleries to the number of exit holes of the first generation. To assess host species effect on the ratios, a Kruskal–Wallis test was performed.

Larval performance. Spearman's correlation coefficients were calculated between number of exit holes and emerging adults for the choice assay and the second generation of the no-choice assay. In all these cases, significant positive relationships were found (r_s in the range 0.73–0.92, $P < 0.001$). Hence, for both choice assay and all generations of the no-choice assay, we used only the number of exit holes to calculate the larval survival rate (i.e. number of exit holes per egg niches). Female fecundity (i.e. number of egg niches per fertile egg galleries), densities of egg niches, larval galleries, exit holes and length of fertile egg galleries were also measured. Tree species effect on these parameters was assessed using a Kruskal–Wallis test. Comparisons of female fecundity and survival rate between the choice and the no-choice assays and comparisons between generations in the no-choice assay were also performed with a Kruskal–Wallis test.

Morphometric analyses were carried out to estimate whether larval host affected the size of emerging adults. Effect of tree species, beetle sex and individual tree on size parameters were investigated using a factorial analysis of variance. Pronotum width data were ArcSin$\sqrt{x}$ transformed to fit in with a normal distribution.

Statistical analyses were performed with R software, version 2.4.1 (R Development Core Team, 2005).

Results

Adult preference

In the choice assay, all tree species were attacked by *P. chalcographus*, although *P. abies* and *P. sitchensis* were more frequently attacked than the other species. Among the 14 logs of each species, 14 *P. abies*, 13 *P. sitchensis*, eight *P. sylvestris*, two *P. contorta* and seven *P. menziesii* were attacked. In the mixed-effect linear model analysis, when *P. abies* was used as the reference, all coefficients associated with other species were negative (Table 1) indicating that other hosts were less selected than *P. abies*, and thus that *P. abies* was the preferred species for the three response variables. *Picea abies* was attacked significantly more often than the other host species, and had a higher density of nuptial chambers and fertile egg galleries (Fig. 1). The presence of other Pinaceae species did not affect the density of attack on *P. abies* because the three response variables did not differ between control test and choice assay. Although differences among the four other species were lower than with *P. abies*, a preference ranking could be drawn from the coefficient values. After *P. abies*, *P. chalcographus* preference decreased from *P. sitchensis* to *P. menziesii* and, finally, *Pinus* species (Table 1). In all host species, most nuptial chambers had only one egg gallery, except for *P. abies*, where polygamous males were observed (2.4 females per male, SE = 0.4).

Bark thickness differed significantly among tree species ($H_{4,71} = 33.00$, $P < 0.001$) and, according to pairwise Kruskal–Wallis tests, two significant groups were distinguished: a group with *P. sylvestris* (0.50 ± 0.04 cm) and *P. contorta* (0.66 ± 0.06 cm) and a group with *P. abies* (0.31 ± 0.02 cm), *P. sitchensis* (0.32 ± 0.02 cm) and *P. menziesii* (0.34 ± 0.02 cm). When each tree species was considered separately, there was no relationship between bark thickness and the densities of attack, nuptial chambers and fertile egg galleries. However, when all species were pooled, there was a significant negative correlation between bark thickness and
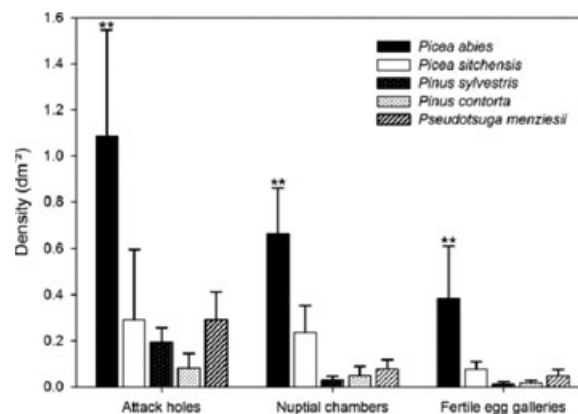

Figure 1 Mean ± SE densities of attack, nuptial chambers and fertile egg galleries of *Pityogenes chalcographus* on five host species, during the choice assay. **Host species significantly preferred by the beetles using a mixed-effect linear model ($P < 0.05$).

the densities of attack ($r_s = -0.30$, $P = 0.009$) and nuptial chambers ($r_s = -0.28$, $P = 0.015$).

In the no-choice assay, 80% of the artificially introduced males in the first generation bored nuptial chambers with egg galleries in *P. abies*, 55% in *P. sitchensis*, 25% in *P. menziesii* and 15% in *Pinus* species. *Picea* species exhibited a significantly higher number of fertile egg galleries than the other species and a higher number of nuptial chambers than *Pinus* sp. (Fig. 2). Emerging adults of the first generation attacked all tree species, although neither nuptial chambers nor egg galleries were observed in *P. sylvestris*; thus, this species was excluded from the performance analyses. For the second generation, intra-host species variability was high and no significant difference was found for the ratios of attack ($H_{4,41} = 7.89$, $P = 0.10$), nuptial chambers ($H_{4,41} = 4.99$, $P = 0.29$) and fertile egg galleries ($H_{4,41} = 5.95$, $P = 0.20$) among host species (Fig. 3).

Larval performance

In the choice assay, performance parameters were greater in *P. abies* than in *P. sitchensis*, although significant differences were found only for larval gallery density and length of fertile egg galleries (Table 2). Fertile egg gallery length, female fecundity, survival rate and exit hole density were significantly higher in *Picea* species than in *Pinus* species. Survival was extremely low in both *Pinus* species. Larval performance in

Table 1 Mixed-effect linear model results constructed with the simple model for three response variables tested based on *Picea abies*

| Modality	Attack density		Nuptial chamber density		Fertile egg gallery density	
	Value	*P*-value	Value	*P*-value	Value	*P*-value
Picea sitchensis	−0.795	0.016	−0.431	0.008	−0.306	0.039
Pseudotsuga menziesii	−0.796	0.016	−0.587	<0.001	−0.336	0.024
Pinus sylvestris	−0.892	0.007	−0.637	<0.001	−0.372	0.013
Pinus contorta	−1.005	0.003	−0.618	<0.001	−0.367	0.014
Control test (*Picea abies*)	−0.223	0.614	−0.021	0.924	−0.159	0.427
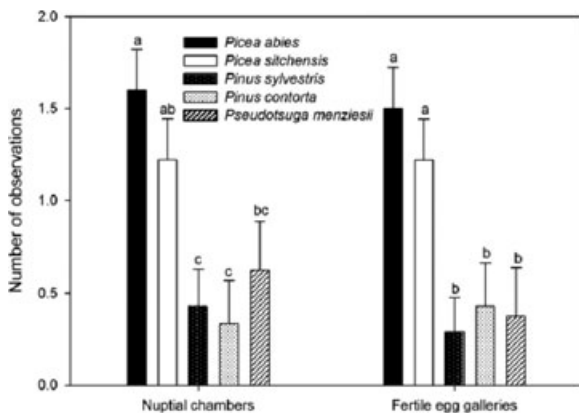
Figure 2 Mean ± SE number of nuptial chambers and fertile egg galleries of *Pityogenes chalcographus* after artificial introduction of insects in logs of five different host species. Bars with the same letter did not differ significantly from each other using a pairwise Kruskal–Wallis test ($P < 0.05$).
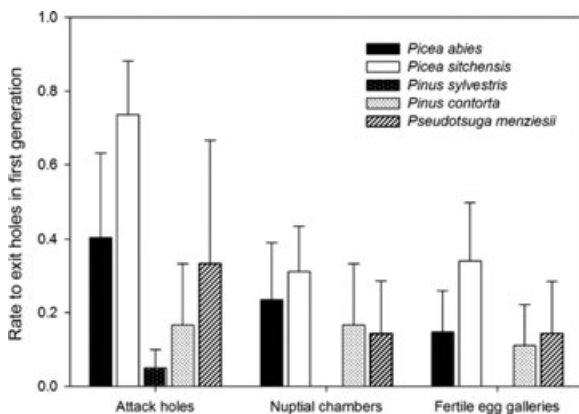

Figure 3 Mean ± SE percentage of attack, nuptial chambers and fertile egg galleries of the second generation calculated on the number of exit holes of a first generation of *Pityogenes chalcographus* that developed on five host species after a no-choice assay. No significant results were found using a pairwise Kruskal–Wallis test ($P < 0.05$).

P. menziesii did not differ from those in *P. sitchensis*, even though female fecundity was initially lower.

Performance parameters did not differ between *P. abies* and *P. sitchensis* in the first generation of the no-choice assay (Table 3). Performance was significantly greater in *Picea* than in *Pinus* species and *P. menziesii*; however, the density of larval galleries did not differ between *P. sitchensis* and *P. contorta*. Fertile egg gallery length did not differ between *Picea* species and *P. menziesii*. In the second generation, there was no difference between *P. abies* and *P. sitchensis* among any of the performance parameters measured (Table 3). In *P. menziesii*, the densities of egg niches, exit holes, and the survival rate was significantly lower than in *P. sitchensis*. Female fecundity and fertile egg gallery length also tended to be lower in *P. menziesii* than in *P. sitchensis*, although not significantly, whereas the densities of larval galleries were similar in these two species. Female fecundity was extremely low and no brood development occurred in *P. contorta*. There

was no difference in performance parameters in any tree species between generations.

Pityogenes chalcographus survival rate did not significantly differ between choice and no-choice assays ($H_{1,118} = 0.64$, $P = 0.42$). However, female fecundity was significantly higher in *P. abies* and *P. sitchensis* (*P. abies*: $H_{1,22} = 5.86$, $P = 0.02$; *P. sitchensis*: $H_{1,22} = 6.39$, $P = 0.01$) in the no-choice assay.

In both choice and no-choice assays, no difference in beetle size (elytra length and pronotum width) was observed among host species (choice assay: elytra length, $F_{4,174} = 1.58$, $P = 0.18$; pronotum width, $F_{4,174} = 0.006$, $P = 0.34$; no-choice assay: elytra length, $F_{4,212} = 1.63$, $P = 0.17$; pronotum width, $F_{4,212} = 1.49$, $P = 0.21$) and individual trees (choice assay: elytra length, $F_{1,174} = 0.49$, $P = 0.48$; pronotum width, $F_{1,174} = 1.23$, $P = 0.27$; no-choice assay: elytra length, $F_{1,212} = 0.02$, $P = 0.88$; pronotum width, $F_{1,212} = 0.01$, $P = 0.91$). However, beetle sex had a significant effect on both variables (choice assay: elytra length, $F_{1,174} = 8.812$, $P < 0.01$; pronotum width, $F_{1,174} = 22.337$, $P < 0.001$; no-choice assay: elytra length, $F_{1,212} = 9.476$, $P < 0.01$; pronotum width, $F_{1,212} = 31.969$, $P < 0.001$). Males were significantly wider and shorter than females (mean male elytra length: 1.22 ± 0.01 mm, mean male pronotum width: 0.75 ± 0.01 mm; mean female elytra length: 1.27 ± 0.01 mm, mean female pronotum width: 0.72 ± 0.01 mm). No interaction among host species, individual tree and beetle sex was found.

Discussion

Picea abies was the most attacked species and the only tree species in which *P. chalcographus* was polygamous. This is congruent with the field observations indicating that *P. abies* is the preferred host of *P. chalcographus* (Chararas, 1962; Zumr, 1992; Grégoire & Evans, 2004) and the presence of the four other tree species did not influence the preference of *P. chalcographus*. *Picea abies* was also the most suitable host for *P. chalcographus* development. In both the choice and no-choice assays, a high number of egg niches, larval galleries and exit holes were observed in this tree species, resulting in a high fecundity and survival rate. The difference in female fecundity between choice and no-choice assays probably resulted from a difference in the age of the beetles used for these assays. The no-choice assay was undertaken prior to the choice assay; thus, beetles used for the choice assay were late-emerging adults. Late-emerging adults have been reported to exhibit a smaller size and lower lipid concentration than early-emerging adults as a result of phloem desiccation and intraspecific competition (Anderbrant *et al.*, 1985; Sallé & Raffa, 2007), which could lead to a decrease in insect fertility (Thalenhorst, 1958; Anderbrant *et al.*, 1985). Insects used for both the choice and no-choice assays were collected from *P. abies* trees. This may have affected adult preference, according to the Hopkins host selection principle, which states that phytophagous insects show breeding and feeding preferences for the plants on which they developed as larvae (Hopkins, 1917; Schlyter & Birgersson, 1999). It also could have influenced the breeding experiment through a maternal effect. However, there was no

Table 2 Mean ± SE performance parameters of *Pityogenes chalcographus* submitted to a host selection assay among five host species in the choice assay

	Picea abies	Picea sitchensis	Pinus sylvestris	Pinus contorta	Pseudotsuga menziesii	H		P value
Fertile egg gallery length (mm)	24.72 ± 1.58[a]	14.54 ± 3.60[b]	6.85 ± 4.53[c]	4.32 ± 2.42[c]	10.99 ± 2.13[bc]	$H_{4,145}$	49.62	<0.001
Larval gallery density (dm^2)	0.84 ± 0.11[a]	0.35 ± 0.15[b]	0.19 ± 0.14[b]	0.04 ± 0.04[b]	0.15 ± 0.07[b]	$H_{4,145}$	44.26	<0.001
Egg niche density (dm^2)	6.55 ± 3.98[a]	1.13 ± 0.64[ab]	0.50 ± 0.50[c]	0.26 ± 0.18[bc]	0.41 ± 0.22[bc]	$H_{4,65}$	14.83	0.005
Female fecundity	9.93 ± 2.22[a]	6.16 ± 1.93[a]	1.89 ± 1.89[b]	2.57 ± 1.75[b]	2.39 ± 1.32[b]	$H_{4,65}$	14.37	0.006
Survival rate	0.38 ± 0.15[a]	0.29 ± 0.12[ab]	0.01 ± 0.01[c]	0.01 ± 0.01[c]	0.07 ± 0.05[bc]	$H_{4,65}$	17.21	0.002
Exit hole density (dm^2)	2.16 ± 0.85[a]	0.94 ± 0.38[ab]	0.07 ± 0.07[c]	0.02 ± 0.02[c]	0.16 ± 0.09[bc]	$H_{4,65}$	15.01	0.005

Groups with the same superscript letter did not differ significantly from each other using a pairwise Kruskal–Wallis test ($P < 0.05$). See text for details on the parameters studied.

Table 3 Mean ± SE performance parameters of *Pityogenes chalcographus* in five host species in the no-choice assay

	Picea abies	Picea sitchensis	Pinus sylvestris	Pinus contorta	Pseudotsuga menziesii	H		P value
First generation								
Fertile egg gallery length (mm)	21.50 ± 2.71[a]	23.86 ± 2.29[a]	12.07 ± 3.88[b]	9.70 ± 4.67[bc]	18.57 ± 4.22[ac]	$H_{4,86}$	12.78	0.012
Larval gallery density (dm^2)	0.86 ± 0.16[a]	0.63 ± 0.17[ab]	0.02 ± 0.02[c]	0.36 ± 0.30[bc]	0.10 ± 0.07[c]	$H_{4,86}$	21.29	<0.001
Egg niche density (dm^2)	4.55 ± 1.37[a]	2.80 ± 0.87[a]	0.29 ± 0.23[b]	0.95 ± 0.77[b]	1.42 ± 0.97[b]	$H_{4,45}$	19.05	<0.001
Female fecundity	26.95 ± 5.05[a]	17.60 ± 3.63[a]	2.10 ± 1.55[b]	4.75 ± 3.42[b]	9.00 ± 6.91[b]	$H_{4,45}$	19.66	<0.001
Survival rate	0.25 ± 0.07[a]	0.42 ± 0.17[a]	0.08 ± 0.08[b]	0.01 ± 0.01[b]	0.01 ± 0.01[b]	$H_{4,45}$	24.19	<0.001
Exit hole density (dm^2)	1.59 ± 0.58[a]	0.87 ± 0.37[a]	0.21 ± 0.19[b]	0.13 ± 0.13[b]	0.11 ± 0.11[b]	$H_{4,45}$	22.20	<0.001
Second generation								
Fertile egg gallery length (mm)	21.33 ± 2.63[a]	24.39 ± 1.76[a]	NA	7.93 ± 2.80[b]	19.85 ± 7.87[ab]	$H_{3,118}$	14.42	0.002
Larval gallery density (dm^2)	0.01 ± 0.01[a]	0.01 ± 0.01[a]	NA	0[b]	0.01 ± 0.01[ab]	$H_{3,118}$	17.71	<0.001
Egg niche density (dm^2)	3.82 ± 2.20[ab]	11.16 ± 4.65[a]	NA	0.36 ± 0.36[b]	2.23 ± 2.23[b]	$H_{3,34}$	9.72	0.020
Female fecundity	14.02 ± 3.74[a]	15.93 ± 3.02[a]	NA	1.50 ± 1.50[b]	5.17 ± 5.17[ab]	$H_{3,34}$	9.74	0.020
Survival rate	0.13 ± 0.06[ab]	0.24 ± 0.06[a]	NA	0[b]	0.02 ± 0.02[b]	$H_{3,34}$	10.48	0.015
Exit hole density (dm^2)	0.13 ± 0.06[ab]	0.24 ± 0.06[a]	NA	0[b]	0.02 ± 0.02[b]	$H_{3,34}$	10.48	0.015

Groups with a same letter did not differ significantly from each other using a pairwise Kruskal–Wallis test ($P < 0.05$). For details on the parameters studied, see text.

difference in breeding performance between generations in the no-choice assay, suggesting that the host on which the previous generations had developed probably had little or no effect.

The results obtained in the present study indicate the existence of a positive relationship between adult preference and larval performance, except for the size of the emerging beetles, which was not affected by the larval host. This positive relationship was probably a consequence of both the extended contact between adults and the host plant prior to and during oviposition and the obligation of larvae to develop where eggs were laid, as expected from the phylogenetic constraints hypothesis. Both preference and performance parameters were high on *P. abies*, whereas tree species having few attacks were also the hosts in which larval performance was the worst. When intermediate levels of adult preference occurred, intermediate or high larval performance was recorded. According to the optimal oviposition theory (Jaenike, 1990), *P. chalcographus* preferentially oviposit into host species on which their offspring perform best but, occasionally, they also lay eggs into less suitable plant species. Alternative hosts of *P. chalcographus* can be ranked depending on both adult preference and larval performance. *Picea sitchensis*, an exotic congener of *P. abies*,

was the second most attacked species, and breeding success was close for these hosts in both the choice and the no-choice assays. Although attack density was lower on *P. sitchensis* than on *P. abies*, *P. sitchensis* provided an adequate substratum for larval development.

Our laboratory observations concur with our field observations in France where attacks by *P. chalcographus* occurred on *P. sitchensis*, but at lower levels than on *P. abies* (C. Bertheau *et al.*, 2009). Similarly, other exotic *Picea* species, such as *Picea pungens*, are often colonized by *P. chalcographus* (Zumr, 1992). Both *Pinus* species assessed in the present study were the less suitable hosts for *P. chalcographus*, especially *P. sylvestris* where the beetle survival rate was so low that no successive reproduction occurred. Field reports mentioned the occurrence of *P. chalcographus* in different pine species, including *P. sylvestris* and *P. contorta* (Balachowsky, 1949; Chararas, 1962; Austarå *et al.*, 1983; Zumr, 1992; Pfeffer, 1994), and frequent attacks of *P. chalcographus* have been reported on trap trees of the exotic *Pinus strobus L.* (Zumr, 1992; C. Bertheau *et al.*, 2009). Nonetheless, except for *P. strobus*, *P. chalcographus* never generates significant damage on these trees, and field surveys using trap trees

reported only very sporadic attacks on *P. sylvestris* (Zumr, 1992; C. Bertheau *et al.*, 2009). This is congruent with the low adult preference and larval performance found for the *Pinus* species used in our assay. The low performance, however, contradicts the results of a previous experimental breeding on *P. sylvestris* (Fuehrer & Muehlenbrock, 1983). Similarly, the low performance observed in the same study in *P. menziesii* disagrees with the results obtained in the present study. In this tree species, *P. chalcographus* exhibited adult preference and larval performance intermediate between those in *Picea* and *Pinus* species or even close to those in *P. sitchensis*. The discrepancy between the results obtained in the present study and this previous experimental breeding may be the consequence of differences in laboratory conditions.

Host preference ranking of oligophagous insects often mirrors the taxonomic relationship among plants, enabling them to colonize related plant species (Schoonhoven, 1991). Some insects, such as the leafhopper *Aphrophora alni*, appear to be able to classify the plant species of their host range with regard to genus and family (Nuorteva 1952). In the present study, the preference of *P. chalcographus* for tree species went to *Picea* species, then to *P. menziesii* compared with *Pinus* species. Few data on the phylogenetic relationships among Pinaceae are available. Classification of Belgian native and exotic Pinaceae, based on morphological and genetic characters, clusters *Pseudotsuga* with *Picea* and *Pinus* in the subfamily of the Pinoideae (Verhaeghe, 2003). Different molecular markers have also shown that these three genera belong to the same clade, although *Picea* and *Pinus* species are genetically closer to each other than to *P. menziesii* (Aaron, 1996; Wang *et al.*, 2000). The preference ranking of *P. chalcographus* in the present study is thus only partially in agreement with this phylogenetic relationship. Taxonomic relatedness could play a role in host selection at the scale of the genus (i.e. within the *Picea* genus) but not at higher taxonomic levels, where other factors could be more decisive.

Among other factors that could influence beetle preference, bark thickness appears to be a good candidate because it was negatively correlated to beetle preference in the present study. The lower attack densities encountered on *Pinus* species compared with *Picea* and *Pseudotsuga* species could be the consequence of thicker bark. This agrees with *P. chalcographus* distribution on trees in the field (i.e. in trunks and branches where the bark is thin) (Balachowsky, 1949; Chararas, 1962). Thus, it appears that *P. chalcographus* seeks similar resources among hosts (e.g. thin bark) rather than phylogenetic relationships. This would explain the high attack rate in the field and the maximum breeding success in experimental breeding of *P. chalcographus* on *P. strobus*, for which bark thickness is comparable with that of *P. abies* (Fuehrer & Muehlenbrock, 1983; Zumr, 1992; C. Bertheau *et al.*, 2009). Further studies including *P. strobus* would help to distinguish the effect of plant taxonomic relatedness from the effect of resource similarity among hosts. Another factor that could also interfere in beetle preference is tree chemistry. Secondary metabolites produced by plants may be somewhat characteristic of a particular genus or even family (Schoonhoven *et al.*, 2005), and host selection mechanisms by bark beetles, including *P. chalcographus*, are complex, although driven to a large degree by plant compounds such as monoterpenes (Chararas, 1962; Byers, 2004). Whether a chemical relatedness among *P. chalcographus* hosts can influence beetle preference remains to be investigated.

Although adult preference and larval performance among different host trees are decisive parameters for assessing the ability of bark beetles to cause extensive damage, they have been poorly studied in Europe (Walker & Ross, 1975; Chararas *et al.*, 1982; Lieutier *et al.*, 1997; Faccoli, 2007). *Pityogenes chalcographus* exhibited a positive relationship between adult preference and larval performance, suggesting that preferred host species are more likely to undergo damage. The preferences among its host range appear to be related to resource similarity (bark thickness) rather than to plant taxonomic relatedness. Resource relatedness to preferred native hosts appears to be an important parameter for consideration in forest management, especially for risk assessment in mixed conifer forests and in exotic conifer stands. The present study also indicates that special attention should be given to *P. sitchensis* and *P. menziesii* because they were adequate substrate for *P. chalcographus* development. Conversely, *P. contorta* did not appear to be a species at risk.

Acknowledgements

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