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# A sampling technique to estimate within-tree populations of pre-emergent *Ips typographus* (Col., Scolytidae)

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**Abstract:** A sampling method was designed to assess within-tree pre-emergent adult populations of *Ips typographus* in Belgium. In a first series of 6 standing, attacked trees, a large number of 1 $dm^2$ samples (56–171 samples, according to tree) were collected and analysed. Sets of samples were selected at random with successive increments of one unit among the samples from each tree, and the mean numbers of beetles and standard deviations in each of these random sets were used to calculate changes in sampling precision as the number of samples in a set increased. For each tree, there was an excellent fit with a power function linking sampling error and number of samples in each set. Fifty random samples per tree allowed estimates of the mean with an error of 9–24%. Further analysis of sample variation along and around the trunks showed that beetle density did not vary around but along the trunks, suggesting that sampling should not be totally random but should take into account longitudinal changes in beetle populations on attacked trees. At each level of each tree, sets of samples were selected at random with successive increments of one unit to calculate changes in sampling precision. At any level along the trunks, taking four 1 $dm^2$ samples yielded estimates with an error inferior to 10%. To validate the conclusions drawn from these results, eight other trees were then sampled at regular intervals along the trunk. A total of 43–56 samples were taken per tree, yielding estimates with a computed error of 9–13% of the mean. Beetle density along the trunks was found to increase linearly along the basal portions of the infested stems (15% of the infested stem), remain constant along the following 65% of the infested stems, and decrease linearly along the terminal 20%. Taking all this information into account, the total pre-emergent beetle population in each tree was estimated. Total beetle production per tree ranged from 35 000–72 000.

## 1 Introduction

The integrated management of bark beetles requires accurate population estimates, to measure changes in time and space, and to evaluate the impact of control methods. Sampling techniques have been designed for a number of species, e.g. *Scolytus ventralis* (BERRYMAN, 1986), *Scolytus tsugae* (SCHENK et al., 1976), *Dendroctonus frontalis* (LINIT and STEPHEN, 1978; MAYYASI et al., 1976a, 1976b; PULLEY et al., 1976, 1977; STEPHEN and TAHA, 1976, 1979), *Dendroctonus ponderosae* (SAFRANYIK, 1988), *Tomicus piniperda* and *Ips sexdentatus* (BOUHOT et al., 1992), *Ips typographus* (WESLIEN and REGNANDER, 1990). Our own work is also concerned with this last species.

The Eurasian spruce beetle, *Ips typographus* L., is well known in the forest entomology literature for the considerable damage it can cause to spruce [e.g. 30 million $m^3$ in Central Europe after World War II (WELLENSTEIN, in ANNILA, 1969), 5 million $m^3$ in Norway during the 1971–82 period (BAKKE, 1983)]. Large scale control campaigns have been developed against this pest, involving sanitation felling, pheromone mass trapping (e.g. BAKKE, 1989; FURUTA et al., 1986; ABGRALL and SCHVESTER, 1987; WESLIEN, 1992) and pheromone monitoring (WESLIEN et al., 1989). In Belgium, severe storms in February 1990 felled about 6 million $m^3$ of spruce and were followed by two successive dry summers. As a consequence, outbreaks developed everywhere in the southern part of the country. Sanitation measures (felling and removal of infested material) and mass trapping (pheromone-baited poisoned trap-trees) were implemented on a national scale by the Forest Administration and alike. Parallel experiments were set up in order to assess the impact of these measures (DRUMONT et al., 1991, 1992).

As these assessments eventually rely on population estimates, the present study concerns the establishment of an accurate and cost-effective method for estimating within-tree populations of pre-emergent adults. In a first approach, a series of trees were sampled in order to analyse pre-emergent adult beetle distribution along and around the trunk, and in order to determine how many samples were needed for obtaining populations estimates whith 80–90% accuracy. This methodology was then successfully validated by sampling a second series of trees.

## 2 Material and methods

### 2.1 First series of trees (establishment of the sampling methodology)

#### *2.1.1 Sampling*

Six attacked trees were sampled (table 1) between 25 and 30 July 1991 (trees 1–4) and 15–30 August 1991 (trees 5–6), at two localities in Southern Belgium (Bertrix and Saint-Hubert, Province of Luxembourg). Circular samples (1 $dm^2$) were taken using a piece of sharpened metal tubing driven into the bark with a hammer. Each sample was kept separately in a plastic bag, brought back to the laboratory and carefully

***Table 1.*** *Description of the trees used for the first series of samplings*

| Tree | Locality | Type of tree[1] | h/h′ (m)[2] | Diameter (cm) | Attacked bark area (dm²) | *Pityogenes chalcographus*[3] |
|---|---|---|---|---|---|---|
| 1 | St-Hubert | T | 3/15 | 40/23 | 1484 | |
| 2 | St-Hubert | T | 4/19 | 39/19 | 1731 | |
| 3 | St-Hubert | T | 4.5/17.5 | 31/19 | 1051 | |
| 4 | Bertrix | T | 5/14 | 40/30 | 989 | >9 m |
| 5 | Bertrix | N | 0.5/19 | 48/22 | 2063 | >16 m |
| 6 | Bertrix | N | 1.5/15 | 46/24 | 1441 | >13 m |

[1] T = ex-trap tree, protected with an insecticide up to 3–4 m but which has been eventually overcome by *Ips typographus*. Infestation started where chemical protection ended. N = normal, unprotected tree, attacked standing.
[2] h and h′ indicate the heights where the attacks of *Ips typographus* began and ended.
[3] Height at which *Pityogenes chalcographus* attacks started.

***Table 2.*** *Sampling on the first series of trees*

| Tree[1] | Longitudinal sample groups | Circular sample groups | | | | | Whole tree |
|---|---|---|---|---|---|---|---|
| | Total no. of samples | No. of rings | No. of ringlets per ring | Distance between rings (m) | h/h′[2] (m) | Total no. of samples | Total no. of samples |
| 1 (III) | 58 | 4 | 3 | 3 | 6/18 | 105 | 151 |
| 2 (II) | 123 | 9 | 2 | 2 | 5/21 | 99 | 171 |
| 3 (II) | 98 | 6 | 2 | 2 | 5/17 | 65 | 123 |
| 4 (II) | 76 | 3 | 2 | 2 | 7/13 | 65 | 127 |
| 5 (I) | 72 | — | — | — | — | — | 72 |
| 6 (I) | 56 | — | — | — | — | — | 56 |

[1] Roman figures between brackets refer to the corresponding part of fig. 1.
[2] h and h′ indicate the heights where the first and last rings where undertaken.

analysed, counting the numbers of individuals of each developmental stage. The presence of *Pityogenes chalcographus* was also recorded, as a competitor potentially influencing host exploitation by *Ips typographus*. According to the individual characteristics of each tree (branches, length of infested portion of the trunk), various numbers of samples were taken (table 2 and fig. 1). In all cases, samples were collected in such a way that possible variations in beetle distribution along and around the trunks were taken into account ('longitudinal' and 'circular' sample groups, respectively). The samples for longitudinal sample groups (1 or 2 disks at each level) were taken at regular intervals of 1 m within each of 4 sectors corresponding to the four cardinal orientations. The samples for circular sample groups ('rings') were taken at larger intervals (2–4 m; see table 2 and fig. 1). Each one of the rings consisted of 2–3 subunits ('ringlets'); the numbers of samples per ringlet varied according to trunk diameter. As these two series of samples partly overlapped, it happened that some samples belonged to both series. Infested bark areas were calculated assuming that the tree trunks were truncated cones.

### *2.1.2 Determination of overall sampling size*

Sets of samples were selected at random among the samples for each tree, with successive increments of one unit (1 dm²), and the mean numbers of adult beetles and standard deviations in each of these random sets were calculated. For each subsample, sampling error was then calculated (SOUTHWOOD, 1966):

$$d = \frac{t \cdot s}{\sqrt{N} \cdot \bar{x}} * 100$$

Where d is the sampling error (in percents of the mean), N is the number of samples, t is the value in Student's *t* distribution corresponding to N, $\bar{x}$ and s are, respectively, the mean and standard deviation of the subsample. This procedure was repeated 3 times for each tree.

## 2.2 Second series of trees (validation of the sampling methodology)

Eight attacked standing trees were sampled (table 3) between 10 and 15 October 1991 in Saint-Hubert, according to the results obtained from analysing the first series of trees (see the 'Results' section). Tables 3 and 4, respectively, describe the trees which were used and the sampling procedure applied.

In the central length of infested bark of each tree, sampling levels were established at regular intervals of 2.5 m, counting upwards from the lower limit of infestation, with 5–6 samples per level. According to the total infested length of each tree (table 3), there were 6–9 levels, and the total numbers of samples in the central infested length ranged from 35 to 45 per tree.

The basal and terminal parts of the infested section of each tree (each less than 2.5 m from the limit of infested bark) were sampled separately, to account for a gradual increase and decrease of beetle density, respectively, from the point were attacks started, and towards the point where they ended. The samples were taken linearly along the axis of the tree, at regular intervals of 25–50 cm from the lower and upper limits of infested bark. The number of samples from these basal and terminal parts ranged from 7 to 14.

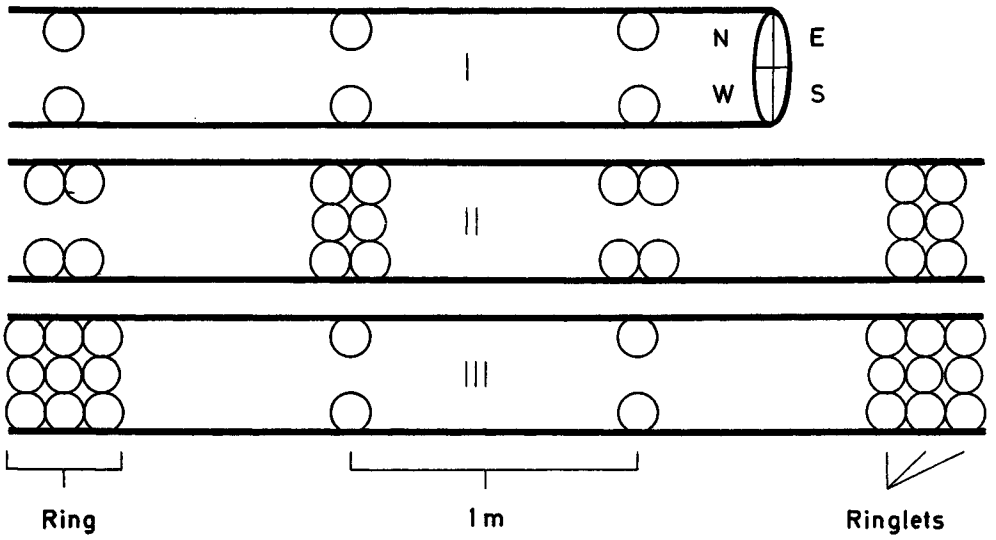


***Fig. 1.*** *Patterns of sampling in the first series of trees*

***Table 3.*** *Trees used for the second series of sampling (validation)*

| Tree | Locality | Type[1] | h/h'[2] (m) | Diameter h/h' (cm) | Area of attacked bark ($dm^2$) | *Pityogenes chalcographus*[3] |
|---|---|---|---|---|---|---|
| 1 | St-Hubert | N | 1.5/18.5 | 46/27 | 2121.3 | >19 m |
| 2 | St-Hubert | N | 0.5/23.5 | 50/20.7 | 2609.8 | >22 m |
| 3 | St-Hubert | N | 1.5/19 | 55/26.1 | 2420 | |
| 4 | St-Hubert | N | 1/16.5 | 52/31 | 2151 | |
| 5 | St-Hubert | N | 0.5/18.5 | 53/33.5 | 2513.7 | >18 m |
| 6 | St-Hubert | N | 1/17 | 48/22.3 | 1877.3 | >17 m |
| 7 | St-Hubert | N | 1/16 | 40/22 | 1458.2 | >18 m |
| 8 | St-Hubert | N | 0.5/17 | 43/21 | 1709 | >16 m |

[1] N = normal, unprotected tree, attacked standing.
[2] h and h' indicate the heights where the attacks of *Ips typographus* began and ended.
[3] Height at which *Pityogenes chalcographus* attacks started.

***Table 4.*** *Sampling on the second series of trees (validation)*

| Tree no. | No. of sampling levels | Central section of tree No. of samples per level | Total no. of samples | Terminal section No. of samples | Whole tree Total no. of samples |
|---|---|---|---|---|---|
| 1 | 7 | 5 | 35 | 9 | 44 |
| 2 | 9 | 5 | 45 | 11 | 56 |
| 3 | 7 | 5 | 35 | 9 | 44 |
| 4 | 6 | 6 | 36 | 7 | 43 |
| 5 | 7 | 5 | 35 | 10 | 45 |
| 6 | 6 | 6 | 36 | 10 | 46 |
| 7 | 7 | 5 | 35 | 14 | 49 |
| 8 | 6 | 6 | 36 | 11 | 47 |

The total numbers of samples per tree varied from 43 to 56 units, with an average of 47 samples per tree.

## 3 Results

### 3.1 First series of trees

#### *3.1.1 Brood stages*

The proportions of the different life stages varied considerably according to the date of sampling. Trees 1–3 contained only callow adults, whereas the other three trees sheltered a proportion of late instar larvae and pupae (tree 4: 47.6% larvae and 32.2% pupae; tree 5: 15.8% larvae and 65.2% pupae; tree 6: 26.8% larvae and 56.5% pupae). Therefore, only trees 1–3 were used for analysing pre-emergent beetle distribution around and along the trunk.

Parasitism (by Braconids and Pteromalids) was negligible (0.21% to 0.65%) in all trees except in tree 4 (13.07%). Tree 4 however, had been excluded from

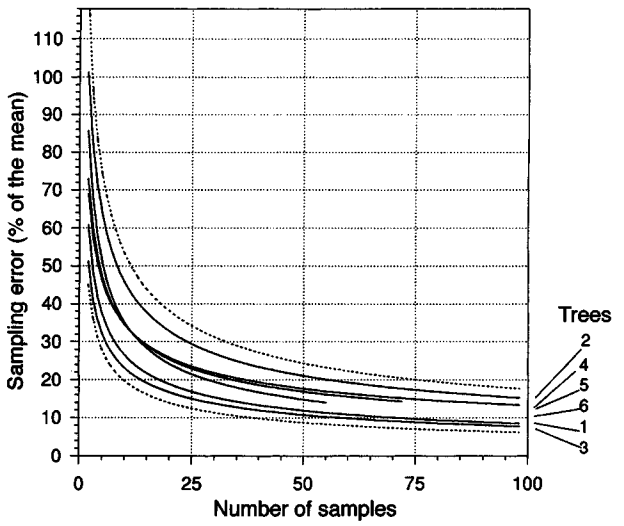


*Fig. 2. Relationships between numbers of 1 dm² samples (taken anywhere on tree) and sampling error in the first series of trees. Each curves was based on three points for any number of samples. Continuous lines: power function relating d to N for the different trees. Dotted lines: extreme 95% confidence limits for the 6 trees; lower dotted line: lower c.i. limit for tree 3; upper dotted line: upper c.i. limit for tree 2*

the analyses of beetle distribution because of its high proportions of larvae and pupae.

### *3.1.2 Determination of overall sampling size*

For each tree, the values for d were plotted against those for N, and a power function was calculated (fig. 2). In all trees, the points and the power function had a very close fit (table 5). Including 95% confidence limits, these functions show that a precision of 76–91% of the mean is achieved with a sample size of 60 bark disks of 1 dm². Sampling errors calculated for trees 4–6 were within the range of those calculated for the other trees, in spite of the large proportions of larvae and pupae in trees 4 and 6 (not taken into account in the analyses), and higher level of parasitism in tree 4.

### *3.1.3 Influence of within-tree distribution on sampling procedures*

Sampling precision might be further increased by stratified sampling if there are within-tree differences in beetle densities. Relative beetle densities (i.e. x/N where x = number of beetles in a sample and N = sum of beetles found in all samples of the same tree) obtained from analysing the 'longitudinal' sample groups from trees 1–3, were submitted to two-way fixed-model analysis of variance after angular transformation ($x' = 2\arcsin\sqrt{x/N}$). There were no significant differences in offspring density between the four sectors of the trees ($F = 0.873$; $P = 0.455$; 3, 362 d.f.). However, there was a highly significant variation along the stem of the trees ($F = 2.156$; $P = 0.004$; 18, 362 d.f.)

A nested two-way analysis of variance of the 'circular' components of sampling (trees 1–3) also revealed highly significant differences between the rings at different heights ($F = 4.308$; $P < 0.005$; 18, 49 d.f.), but not between the ringlets within the rings ($F = 1.072$; $P > 0.05$; 49, 475 d.f.), suggesting homogeneity at any given level on the trunks.

To account for these variations in beetle density along the stems, sampling would need to cover the whole length of attacked bark on the trees. Sampling precision at any level along the trunk was determined separately in trees 1, 2, 3 by randomly taking several (3–15) sets of samples of increasing size at each level (ring) and plotting relative error against number of samples within each ring. Again, these figures fitted extremely well with power functions (fig. 3). Estimates yielded by sets of five samples within-ring had an error inferior to 7% of the mean. In the second series of sampling, 5–6 samples per level were therefore taken.

## 3.2 Second series of sampling

### *3.2.1 Brood stages*

Four out of the eight trees examined during the second series of sampling sheltered 100% adults (trees 1, 3, 4, 7); some larvae and pupae were found in tree 2 (respectively 0.5% and 1%), tree 5 (8.5% and 5%), tree 6 (0% and 8%) and tree 8 (1.4% and 22%). Parasitism was never higher than 1%.

### *3.2.2 Validation of the sampling methodology*

The relative errors (d) calculated from the samplings ranged from 9.28% to 13.12% (table 6). They match with the maximum range calculated from the first series

***Table 5.** Relationship between calculated sampling error and number of samples*

| Tree | Calculated error d[1] Lower 95% conf. interval limit | Average | Upper 95% conf. interval limit | $r^2$ | d.f. | p | Number of sets[2] |
|---|---|---|---|---|---|---|---|
| 1 | $77.678.N^{-0.5242}$ | $84.489.N^{-0.5019}$ | $91.918.N^{-0.4796}$ | 0.87 | 295 | <0.0005 | 3 × 100 sets |
| 2 | $138.357.N^{-0.5281}$ | $150.210.N^{-0.5067}$ | $162.630.N^{-0.4853}$ | 0.88 | 295 | <0.0005 | 3 × 100 sets |
| 3 | $63.372.N^{-0.5074}$ | $70.146.N^{-0.4804}$ | $77.643.N^{-0.4535}$ | 0.81 | 295 | <0.0005 | 3 × 100 sets |
| 4 | $78.181.N^{-0.4584}$ | $90.678.N^{-0.4190}$ | $105.172.N^{-0.3797}$ | 0.60 | 295 | <0.0005 | 3 × 100 sets |
| 5 | $84.101.N^{-0.4948}$ | $97.994.N^{-0.4507}$ | $114.156.N^{-0.4067}$ | 0.66 | 211 | <0.0005 | 3 × 71 sets |
| 6 | $109.194.N^{-0.5754}$ | $122.180.N^{-0.5405}$ | $136.710.N^{-0.5055}$ | 0.85 | 160 | <0.0005 | 3 × 54 sets |

[1] Values obtained from the power functions linking numbers of random samples in a set and errors in sets of samples (see text and fig. 2).
[2] Each set made of samples selected at random, with successive increments of one unit (see text).

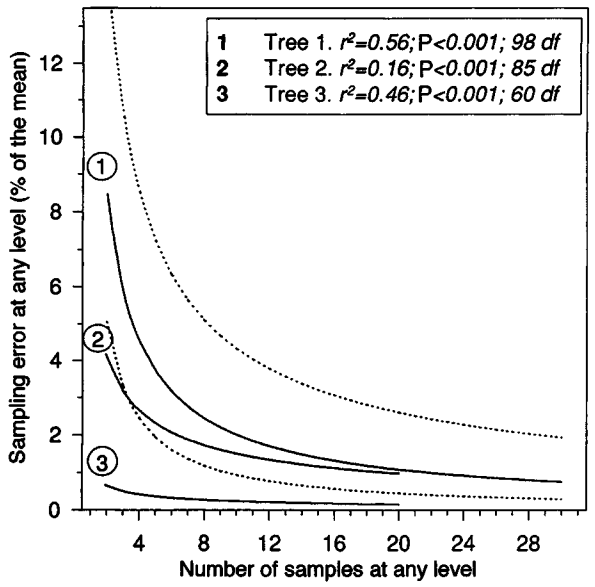


***Fig. 3.*** *Relationship between numbers of 1 dm² samples per level on the trees and sampling error (first series of trees, trees 1–3). 95% confidence limits are also given for tree 1 (dotted lines)*

of samplings (lower 95% confidence limit for tree 3; upper 95% confidence limit for tree 2, see table 5).

*3.2.3 Brood distribution along the trees*

Analysis was performed only on the second series of trees, where most of the insects were at the adult stage. The mean brood densities counted at each of the sampling levels and in both the basal and terminal zones of the trees are shown in table 7. In these latter two zones, the densities were generally lower than the mean densities in the central sampling zone but, in most cases, they were similar to the density observed in the first and last sampling levels within the central zone.

Regression analysis between densities and positions on the trees (all trees together) showed a central zone, between the 15% and 80% of the normalized infested length of the trees, in which no trend was found ($r^2 = 0.018$; $P > 0.05$; see fig. 4b). Beyond the limits of this section, there was a gradual, linear change in brood density. The value of $r^2$ for this change becomes significant from 15% of the normalized length downwards ($r^2 = 0.38$; 78 d.f.; $P < 0.05$; see fig. 4a) and from 80% of the normalized length upwards ($r^2 = 0.51$; 89 d.f.; $P < 0.05$; see fig. 4c).

The inferior limit of the central zone did not vary consistently between trees when they were examined individually, and ranged from 11% to 20% of the normalized infested length. However, a greater variation in the superior limit was observed, ranging from 60% to 88% of the normalized infested length of the trees.

*3.2.4 Brood densities and estimation of within-tree populations*

The average brood densities in the three zones and in the whole tree are shown in table 8. Brood density per tree varied from 18 to 28 *Ips*/dm², with an average of 22.67/dm² per tree (s.d. = 3.01).

The estimation of the total within-tree population corresponds to the sum of the three estimated populations (basal, middle and terminal zones) in each tree. Population in each zone was calculated as the product of the zone's estimated density by its total bark area. Total pre-emergent population per tree varied between 34 847 and 71 828 young adults per tree, with an average of 48 470 (s.d. = 12 530).

## 4 Discussion

The analysis of the first sampling series allows us to assume that there are no differences in offspring distribution around the infested trunk of the tree, and that variations in beetle density occur along the axis of the attacked standing trees. This is in agreement with the results of Weslien and Regnander (1990), who recorded reduced attack density in the lowest section of the trees. Our own results demonstrate that both basal and terminal zones of the infested trees (respectively *c.* 2.5 m and 3.5 m) produce less broods than the central zone. In spite of variations in brood density along the central zone (starting at 15% and ending at 80% of the normalized infested length), no gradient was registered along this zone. In studies undertaken on *Dendroctonus frontalis* (Stephen and Taha, 1976), the smallest densities have also been registered in the terminal zones of the trees. To this respect Mayyasi et al. (1976b) indicate that in the central zone the characteristics of the environment (bark thickness, phloem temperature and moisture level) determine a habitat more homogenous and more suitable for development than in the terminal zones.

Sampling precision was not sensitive to the presence of late immature stages in trees 4–6, as can be seen in table 5 and fig. 2. The goodness-of-fit to power functions for trees 4–6 (as expressed by the coefficients of deter-

***Table 6.*** *Relative error (% of the mean) in the second series of sampling*

| Tree No | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| Number of samples | 44 | 56 | 44 | 43 | 45 | 46 | 49 | 47 |
| Range of error in 1st series[1] | 9.3–29.5 | 8.2–23.1 | 9.3–25.9 | 9.4–26.2 | 9.2–25.6 | 9.1–25.4 | 8.8–24.6 | 9–25.1 |
| Observed error | 12.06 | 10.41 | 13.12 | 12.31 | 12.66 | 9.28 | 12.1 | 11.7 |

[1] Determined using the extreme values from equations in table 5 (lower 95% confidence limit for tree 3; upper 95% confidence limit for tree 2) corresponding to numbers of samples taken from each tree in the second series.

***Table 7.*** *Density of pre-emergent adults (mean* Ips/$dm^2 \pm sd$*) in the second series of samplings*

| Tree no. | Sampling levels of central zone 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | Terminal zones[1] B | T |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 31.40 ±8.87 | 29.20 ±4.45 | 31.80 ±7.44 | 25.40 ±4.22 | 26.00 ±4.24 | 23.40 ±6.34 | 20.60 ±3.61 | | | 23.27 | 17.76 |
| 2 | 19.80 ±2.93 | 25.60 ±8.21 | 25.80 ±8.30 | 26.60 ±2.65 | 25.20 ±3.19 | 24.20 ±3.31 | 25.60 ±4.03 | 24.00 ±1.55 | 13.14 ±2.06 | 11.70 | 16.67 |
| 3 | 19.00 ±2.24 | 27.60 ±5.08 | 27.00 ±8.15 | 33.00 ±7.13 | 21.40 ±7.06 | 24.00 ±5.76 | 18.40 ±3.5 | | | 12.43 | 16.8 |
| 4 | 28.83 ±9.04 | 42.83 ±10.40 | 34.67 ±4.61 | 42.67 ±7.32 | 36.30 ±5.62 | 30.33 ±4.96 | | | | 14.76 | 27.16 |
| 5 | 33.60 ±6.95 | 26.60 ±6.53 | 32.80 ±10.44 | 40.00 ±7.29 | 30.20 ±9.99 | 28.20 ±7.63 | 17.20 ±7.63 | | | 33.84 | 19.70 |
| 6 | 15.50 ±1.26 | 24.50 ±1.89 | 23.83 ±3.58 | 27.67 ±3.77 | 25.83 ±7.17 | 26.33 ±3.09 | | | | 16.42 | 24.78 |
| 7 | 28.50 ±5.74 | 26.00 ±7.90 | 29.33 ±7.18 | 23.83 ±2.54 | 16.00 ±3.11 | 13.50 ±2.81 | | | | 20.05 | 17.72 |
| 8 | 26.50 ±6.37 | 23.50 ±4.50 | 26.83 ±9.57 | 30.17 ±3.83 | 36.50 ±3.49 | 23.33 ±2.64 | | | | 15.20 | 16.27 |

[1] B, T. Basal and terminal portions of the trees (respectively 15% and 20% of the trees' normalized length of infested stem).

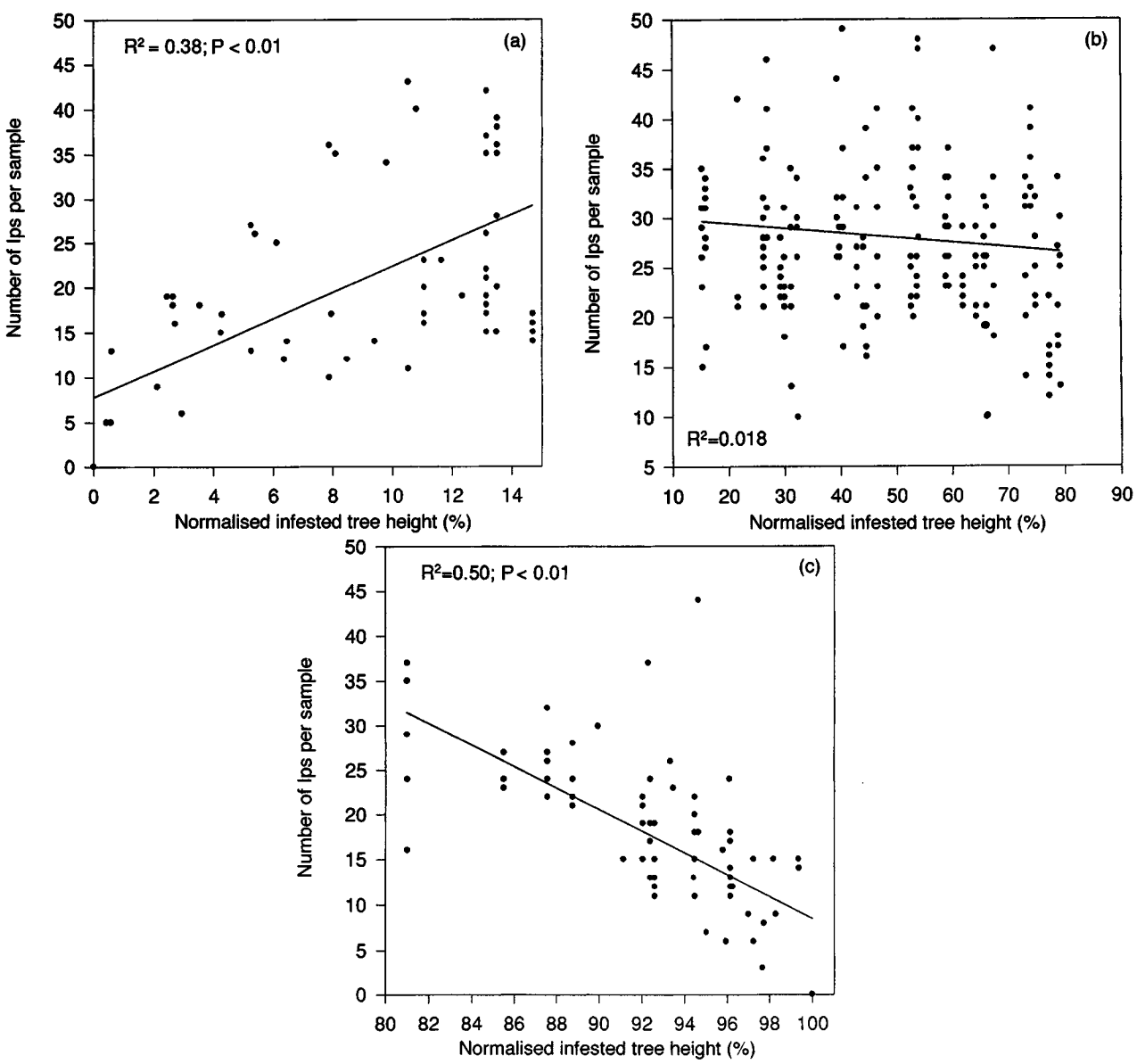


*Fig. 4. Variations of beetle density along the trunk of infested trees. (a) Lower 15% of the infested section. (b) Middle part (15.5% – 79.3%) of the infested section. (c) Upper part (> 80%) of the infested section*

***Table 8.*** *Density of pre-emergent adults in different regions of the trees and total estimated within-tree population*

| Tree no. | Tree zones Basal[1] | Central[2] | Terminal[1] | Whole tree | Estimated population |
|---|---|---|---|---|---|
| 1 | 23.27 | 28.56±6.63 | 17.76 | 23.44 | 49,701 |
| 2 | 11.70 | 25.29±5.19 | 16.67 | 20.84 | 54,363 |
| 3 | 12.43 | 27.25±6.98 | 16.80 | 22.18 | 53,670 |
| 4 | 14.76 | 36.79±9.41 | 27.16 | 24.09 | 51,826 |
| 5 | 33.84 | 33.57±9.15 | 19.70 | 28.29 | 71,170 |
| 6 | 16.42 | 25.63±4.49 | 24.78 | 17.67 | 33,143 |
| 7 | 20.05 | 26.92±6.56 | 17.72 | 22.03 | 34,879 |
| 8 | 15.20 | 27.81±7.12 | 16.27 | 22.82 | 39,004 |

[1] Calculated for mid-point of basal or terminal zone, from regression equations for each tree.
[2] Mean *Ips*/dm$^2$ ± sd, calculated from all individual samples in central zone of each tree.

mination $r^2$) was as good as for the other trees, and the power functions themselves (as well as their 95% confidence limits), are intermediate between those for trees 2 and 3. Mortality between late larval stages and pre-emergent adult stage did not appear to have influenced beetle distribution within the trees. Similarly, parasitism in tree 4 had no influence on sampling error. However, as parasitoids usually are not randomly distributed in tree (see, e.g. DAHLSTEN, 1982 and references therein), higher levels of parasitism still might influence bark beetle within-tree distribution. Future work should address attacked trees with high levels of parasitism.

The results from sampling the second series of trees appear to validate the conclusions resulting from sampling the first series: 43–56 samples (1 dm$^2$) per tree, distributed in groups of 5–6 at regular intervals along the infested portion of the trunks yielded population estimates with an error less than 15% of the mean. In terms of time and labour, this sampling procedure is practically acceptable for population estimates at the tree level. At the stand level, a less intensive procedure would still have to be designed. Our results are valid for pre-emergent beetle populations in summer or in autumn. In the spring, after the insects have overwintered in bark or litter, winter mortality and changes in spatial distribution are very likely to affect sampling precision. Adapted sampling techniques should be specifically designed for post-winter populations.

The estimated average total pre-emergent population per tree (48 470 ± 12 530) was greater than reported by WESLIEN and REGNANDER (1990), who observed average populations of 16 000 ± 3100 beetles per tree with d.b.h. 30 cm and above. These large differences may be due to tree size as, in our study, the trees sampled had a d.b.h. ranging from 38 cm to 55 cm (average: 46 cm ± 4.9 cm). This hypothesis is supported by the fact that our data, pooled with data recalculated from WESLIEN and REGNANDER (1990), show a good linear relationship between numbers of pre-emergent beetles and areas of transversal trunk sections at 1.5 m used as indicators of total bark areas (fig. 5). However, this relationship is only indicative, as other components of tree total bark area (tree height and tapering) were unknown for the Swedish data, as these latter are only average values, and as factors such as parasitism and predation are neglected.

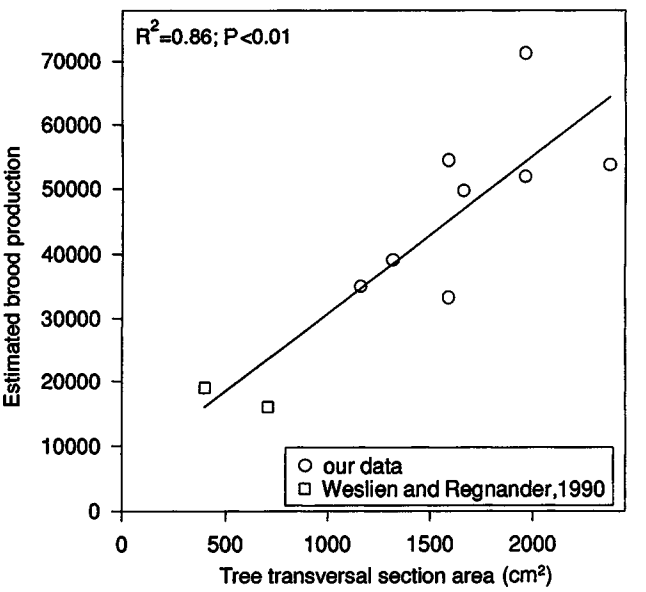


***Fig. 5.*** *Relationship between offspring production and area of transversal trunk section at 1.5 m, as an indicator of total bark areas (fig. 5). Our data and data recalculated from* WESLIEN and REGANDER (1990)

Making the conservative assumption that 2000–10 000 beetles colonize a same new tree, one should expect that the average 50 000 pre-emergent *Ips typographus* produced by each tree in our study should be able to kill 5–25 new trees after emergence. For insects produced in spring and emerging in summer (first generation), this estimate might prove true and could explain the fast population growth observed in some outbreaks. However, insects emerging in the autumn (second generation insects) have to overwinter in bark or litter, and meet severe mortality. In the spring, only a fraction of the initial population would be able to colonize new trees. The extent of winter mortality could be appreciated when sampling procedures to study winter or spring populations are developed.

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