

Effect of climate change on population dynamics of bark beetles: relationships between temperature and development rate of Ips sexdentatus (Boern.)

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Biology and Ecology for Forest, Agriculture and Environment

MSc Major

FORESTS AND THEIR ENVIRONMENT

Effect of climate change on population dynamics of bark beetles: relationships between temperature and development rate of *Ips sexdentatus (Boern.)*



Photo : Iñaki Etxebeste

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1. Introduction

Global warming is now considered a reality and a major threat to ecosystems. In Europe the mean annual temperature has already increased in the last century compared to the past 500 years (Luterbacher et al. 2004) and projections by the intergovernmental panel on climate change (IPCC) predict that it might further increase by 1C° to 2 C° by 2100 (IPCC, 2013).

Forest ecosystems seem to be particularly sensitive to the potential effects of global warming because they cannot adapt rapidly to environmental changes due to the long lifespan of trees (Lindner et al. 2008). A recent study on the potential effects of climate change on European forest ecosystems from different bio climates have been compiled by Lindner et al (2010). It suggests that in the Northern and western part of Europe the increased CO_2 level and higher temperatures might result in longer vegetation season and better forest growth, while the negative effects will outweigh these positive effects in South Eastern Europe and Mediterranean regions, where the productivity is expected to decrease due to drought and fire events. However in all regions the occurrence of biotic attacks such as pest outbreaks is expected to increase (Lindner et al. 2010; Netherer and Schopf. 2010).

Contrary to trees, the life history traits of poikilothermic organisms like forest insects allow rapid adaptation to climatic conditions. They can rapidly respond to increasing temperature by reducing their development time and improving their reproductive success, which result in larger population growth rate and then higher probability of outbreak (Ayres and Lombardero. 2000; Lieutier. 2004; Netherer and Schopf. 2010). Increased temperature can also influence the spread of insect population into new areas, where they were absent due to unsuitable climatic conditions (Lindner et al. 2008; Seidl et al. 2007). Recently insect pest range shifts have been reported on coniferous pests such us bark beetles in North America (Ungerer et al. 1999; William and Liebhold. 2002) or the pine processionary moth *(Thaumetopoea pityocampa)* in Europe (Battisti et al. 2005). Abiotic disturbances such as fire, storm or severe drought also offer large amount of deadwood, which represents suitable resources on which some insects can build up their populations (Wermelinger. 2004; Allen et al. 2010; Rossi et al. 2009). Less rainfall and higher summer temperature is also likely to result in physiologically stressed/weakened trees, which can be less resistant to insect herbivores (Rouault et al. 2006; Netherer and Schopf. 2010; Jactel et al. 2012).

Taken all together pest outbreaks can have devastating impacts on forest ecosystems, especially on timber production (EFI. 2010; Spiecker. 2003), carbon sequestration, water and biodiversity conservation (Seidl et al. 2008) and on the function of protective forests (Martikainen et al. 1999). Thereby there is an increasing demand to study how poikilothermic insects, whose life traits are temperature dependent, will react to the potential effect of global warming. This is particularly the case for bark beetles (scolytids), since most of their recent outbreaks have been attributed to warmer conditions such as in British Columbia - Canada (Williams and Liebhold. 2002; Logan et al. 2003) and in the Bavarian National Park - Germany (Laush et al. 2013; Wermelinger. 2004), the Sumatra National Park - Czech Republic (Jonášova and Prach. 2004) and the Retezat National Park - Romania (personal communication from Gabriela Isaia). Populations of bark beetle species like *Ips typographus* (Coleoptera: Scolytinae) are known to respond positively to warmer temperatures through faster development time (Wermelinger and Seifert. 1998) and thus increased voltinism *i.e.* more generations per year (Seidl et al. 2007; Jönsson et al. 2007, Facolli. 2011). Phenological models also predict that bark beetle species will expand their altitudinal and longitudinal range in response to global warming (Baier et al. 2007; Seidl et al. 2007, 2011; Jönsson et al. 2009, Marini et al. 2012).

In order to estimate how climatic change will affect bark beetles outbreaks range, frequency and intensity, various statistical modeling tools can be used. The available models are based either on correlation between current species distributions and climatic variables (William and Liebhold. 2002; Logan et al. 2003) or on mechanistic relationships between temperature and species – specific physiological responses (Ungerer et al. 1999, Battisti et al. 2005, Baier et al. 2007; Seidl et al. 2007, Jönsson et al. 2009).

The six toothed bark beetle *Ips sexdentatus (Boerner)* (Coleoptera: Scolitinae) is the most common species of pine forests in the Mediterranean region of France, Spain, Portugal, and Greece (William. 2011) where it mainly feeds on *Pinus pinaster*, *P. nigra* and *P. heldreichii* (EPPO n.d). In Northern Europe (incl. France, Sweden, Finland) the beetle is mainly found on *Pinus sylvestris*, while in southern Russia, Turkey, Greece and Georgia it occurs on *Picea orientalis* (Chararas, 1962). A recent study in France on the colonization of exotic conifers by indigenous bark beetles has reported *I. sexdentatus* for the first time on *Pseudotsuga menziessii (*Douglas fir*)* and *Tuja plicata* (Bertheau et al. 2009). *I. sexdentatus* is one of the largest species of the *Ips* genus with a body size of 7 - 8mm in length (IEFC, 2002). Adult females and males have six spines at each side of the elytra declivity. Females have a longitudinal stridulatory organ on the upper hind part of the head (Chararas, 1962) that allows their identification.

In *I. sexdentatus* the male adult initiates the attack on tree trunk, bores a hole through the bark and builds a mating room under the bark in the phloem before to attract females by its sex pheromones (ipsdienol) (Lieutier. 2004; Gitau et al. 2013; Etxebeste et al. 2012). Since the beetle is polygamous, the sex ratio can be 1 male: 4 females to 1:5 (Chararas 1962; Marcu 2005). After mating, the females construct longitudinal galleries depositing each egg into an individual niche on both sides of the gallery. On average 12-40 eggs are laid by female (Chararas, 1962; Jactel et al. 1991). After the eggs hatch, larvae feed on phloem and build larval galleries, which are usually perpendicular to the maternal gallery (Schwenke, 1974). The length of the maternal gallery can be up to 1m long (Shwenke, 1974; IEFC, 2002). The insect has only one generation per year in northern Europe, two generations in central areas of Eurasia and four to five generations in Mediterranean and other areas with long warm summer (Chararas, 1962; Schwenke, 1974; Lèvieux et al, 1985).

Ips sexdentatus is considered a secondary pest of pine plantations in Europe; attacking mainly physiologically weakened trees (by water stress or previous insect defoliations for example)(Schwenke, 1974;Chararas, 1962). The extent of damage therefore depends on tree vigor, host tree resistance and on the number of beetles attacking trees (Jactel and Lieutier. 1987). Primary attacks of living trees occur when pioneer beetles manage to recruit sufficient number of individuals through the release of aggregation pheromone (Lieutier et al, 2004). *I. sexdentatus* outbreaks are often associated with abiotic disturbances such as windstorm or extended forest fires. For instance a recent study has reported that after a devastating windstorm (storm Klaus in 2009 in the Aquitaine region- France) has affected 43.1 million cubic meters of maritime pine, an additional 3.9 million cubic meters were lost due to *I. sexdentatus* damage (EFI, 2010).

While the European spruce bark beetle (*I. typographus*) - the most destructive pest of European coniferous forest (Wermelinger, 2004) - have been intensively studied, there are only few and old studies about the population dynamics of *I. sexdentatus* (Chararas, 1962; Lévieux et al. 1985; Vallet, 1981; Shwenke, 1974) including developmental rate, developmental thresholds, thermal requirement for one generation or the effect of temperature on brood development. However, predicting and forecasting how temperature affects its population dynamics would be highly desirable for current and future prevention techniques and pest management purposes.

Thus the main objectives of this study were:

(1) to determine the thermal requirements (lower developmental threshold) and developmental time (cumulated degree days) for *I. sexdentatus* by performing breeding trials at different temperatures under controlled laboratory conditions;
(2) to calculate the theoretical number of generations per year (voltinism) based on temperatures recorded over the last twenty years in the Aquitaine region;
(3) to estimate the interactive effects of temperature and breeding substrate (pine phloem) quantity and quality on the number of offspring (young adults) and their individual fitness.

2. Material and methods

2.1 Rearing conditions

Climatic chambers were programmed with fluctuating temperatures in order to mimic the natural conditions. We used as reference the climatic conditions of the Aquitaine region from where beetles were originating. Data were retrieved from the database of the INRA - Cestas meteorological station over a 18year period (1996-2013). According to these data, the flight activity of I. sexdentatus (maximum temperature Tmax > 18°C) was almost continuous from April to October, and this period corresponds to flight activity of the beetle (Vallet, 1981 cited by Lévieux et al 1985; Jactel, 1999). Therefore we used the thermal and light conditions of these months for programming the climatic chambers. The temperature followed a sine curve with a 24h period, fluctuating between the minimum temperatures (Tmin) at midnight and maximum (Tmax) temperature at 13 p.m., with an increment of 2°C every two hours. In all climatic rooms we adjusted the photoperiod to the average one of the corresponding month and set up the relative humidity to 60-75% (see Table1).

Table 1. Summary table illustrating the programmed temperature regimes and photoperiod (day and light conditions) used for programming of climatic chambers

MONTHS	APRIL	MAY	JUNE	JULY	AUGUST	AUGUST + 2°C
PHOTOPERIOD	L: D- 13:11	L: D- 14:11	L: D- 16:18	L: D- 15:19	L: D- 14:11	L: D- 17:7
MEAN TEMPERATURE	12 C°	15 C°	18 C°	21 C°	23 C°	25,5 C°
HOURS	TEMPERATURE °C	TEMPERATURE °C	TEMPERATURE °C	TEMPERATURE °C	TEMPERATURE °C	TEMPERATURE °C
1	6	10	12	14	15	17
2	6	11	14	17	18	17
3	8	11	14	17	18	20
4	8	13	16	19	21	20
5	10	13	16	19	21	23
6	10	15	18	21	24	23
7	12	15	18	21	24	26
8	12	17	20	23	27	26
9	14	17	20	23	27	29
10	14	19	22	25	30	29
11	16	19	22	25	30	32
12	16	21	24	27	30	35
13	18	21	24	27	30	35
14	18	19	22	25	30	35
15	16	19	22	25	27	32
16	16	17	20	23	27	29
17	14	17	20	23	24	29
18	14	15	18	21	24	26
19	12	15	18	21	21	26
20	12	13	16	19	21	23
21	10	13	16	19	18	23
22	10	11	14	17	18	20
23	8	11	14	17	15	20
24	8	10	12	14	15	17

In total we tested 6 different temperature regimes, which correspond to the current ones observed in April, May, June, July and August respectively plus an additional regime corresponding to current August temperatures + 2°C. In general in the report we will refer to the mean temperature regimes (Tmean = 12°C, 15°C, 18°C, 21°C, 23°C and 25,5°C respectively).

Three temperature regimes (12°C, 15°C, 18°C) were programmed with FRIOCELL climatic chambers and the others (21°C, 23°C and 25.5°C) with Snejder Labs Microclima Series chambers.

2.2 Breeding substrate

The rearing material was chosen according to the breeding substrate preference of the beetle, thus we choose living maritime pine trees and then logs of ca. 25cm in length and 15cm in diameter with cracked and thick bark. In order to evaluate how phloem quality might affect beetles' development and fitness we selected three different maritime pine (*P. pinaster*) trees. The trees were collected from a maritime pine stand at the INRA centre in Cestas, France (44°44'43"N; 0°40'52"W) in February 2014 (Appendix, Photo 1). Logs were cut and taken back to the laboratory, where both ends were covered with paraffin wax to minimise desiccation. On the following day the bolts were further cut along four radial sections thus resulting in four quarter logs of 20cm length (Appendix, Photo 2).

Quarter log features including width (ca. a quarter of the perimeter, cm), length (cm), bark thickness (mm) and phloem thickness (mm) were measured for each individual bolt prior paraffin coating (Appendix, Photo 3). The waxed logs were stored in deep freezer until beetle inoculation. Logs from the three trees were systematically allocated to the six climatic conditions according to the following experimental design: 6 temperature regimes x 3 trees x 6 logs (replicates) = 108 logs

2.3. Insect rearing

Adult insects were collected in the Landes de Goscogne forest in autumn 2013. Before inoculation the insects were sexed by listening to the "stridulating noise" produced by females. The inoculation of male insects took place on the 5th of March. Prior inoculation the bark was gently smoothed and a 8 mm holes was drilled through the bark surface to the phloem (Appendix, Photo 4). In order to prevent beetle's escape, we covered the entrance hole with a transparent capsule (Appendix, Photo 5). We waited for 24 hours until male insects excavated a nuptial chamber. Presence of frass around the entrance hole or within the capsule was the result of boring activity, a sign for successful beetle's installation (Appendix, Photo 6). Only 13 out of the 90 bolts had an escaped or dead male beetle. The beetles died mainly due to resin pressure of the fresh bolt, which is a protection mechanism of coniferous trees against insects and pathogens. Escaped and dead beetles were substituted with new insects.

On the same day, female beetles were measured with a precision balance (Mettler Toledo, Semi- Micro MS205DU) for the fresh weight, and inoculated at room temperature, i.e. put in the nuptial chamber (Appendix, Photo 7). Although the insect is polygamous we used 1:1 sex ratio in our experiment in order to avoid intraspecific competition for food (phloem) amongst offspring beetles. Female ID was noted on the label of the bolt in order to keep track of female's identity (parent) for further measurements (Appendix, Photo 9). In order to assess beetles' activity and prevent them from escape, the inoculated bolts were introduced into mesh bags with a transparent collector on which the log characteristics and female number

were also noted (Appendix, Photo 10) Then, the bolts where transferred into the programmed climatic chambers (Appendix, Photo 11).

2.4 Life traits of offspring beetles

The climatic chambers were inspected on a daily basis. Emerging young adults (offspring) were collected from May to August 2014, and kept separated per climatic room and bolt of origin. Individual emerging beetles were then sexed, measured and placed in individual tubes with a small piece of paper and stored in the freezer until further measurements (Appendix, Photo 12).

In order to test the effect of temperature and breeding substrate on the fitness of the offspring, the following characteristics were measured on each emerging young adult: sex, fresh weight (g), dry weight (g), elytra length (mm) and elytra width (mm). Additionally the emergence date of the first and last offspring (determined after a two weeks period when there were no more emerging beetles) from each bolt was noted in order to calculate the developmental time of the brood for each climatic condition.

2.5. Statistical data analysis

2.5.1. Defining the lower developmental threshold (LDT) and sum of degree days (K) for complete development

A linear regression analysis was used to determine the relationship between development rate and programmed temperature values (Tmean) within the linear range. Straight lines were fitted using weighted least squares analysis (due to uneven number of bolts with successful insect development amongst climatic chambers). We defined the developmental rate as the inverse number of days (d) required for complete development, i.e. from egg to young adult, (1/d) (Wermelinger & Seifert. 1998, Bentz and Logan. 1991). The linear regression equation is at follows $1/d = a + b\ Tmean$ (Campbell et al.1974; Wermelinger & Seifert.1998; Naves& Sousa. 2009). The lower threshold temperature for development (LDT) was estimated from the x-intercept point of regression equation as $LDT=- a/b$.

We estimate the thermal requirement (sum of degree days for the full development of insects) with three different approaches.

1) The average thermal sum K_1 was estimated as the reciprocal value of the slope b of the linear regression line: $K_1=1/b$ (Campbell et al. 1974; Wermelinger & Seifert. 1998).
2) The thermal constant K_2 was estimated according to "the law of total effective temperatures" often referred as the cumulative degree day approach which corresponds to the accumulated degree days that are needed to complete a particular developmental stage (Damos &Savopoulou-Soultani. 2012): $K_2 = d \times (Tmean\text{-}LDT)$, where d is the developmental time or duration, Tmean is the mean temperature of the climatic chamber and LDT is the lower developmental threshold. Because our climatic chambers were programmed with fluctuating temperature regimes we used the programed temperature regimes minus the lower developmental thresholds to calculate the daily heat sum in each climatic chamber:
   $K_2 = \sum_{i=1}^{24} \frac{(T_i - LDT)}{24}$ where Ti equals the temperature with i^{th} hour of the day
3) The sine wave method (which corresponds to constant K_3) uses the daily minimum (Tmin) and maximum temperatures (Tmax) to reproduce a sinusoidal curve over a 24-hour period (mimicking natural daily fluctuations) and estimate the degree-day by calculating the area above the threshold and below the curve (Zalom et al. 1983; Roltsh et al, 1999). To

estimate it we used the IPM online DD model developed by the University of California (http://www.ipm.ucdavis.edu/). The model requires the lower developmental threshold, daily minimum and maximum air temperatures.

2.5.2. Estimation of the number of generations / year from 1996 - 2013

Sum of degree-days for total development (DD) was calculated using the averaging method that is the most often used, especially in simulation models (McMaster and Wilhelm, 1997, Zalom et al, 1983, Damos and Savopoulou- Soultani, 2011).

The equation is $DD = ((Tmax + Tmin)/2) - LDT$; where Tmax and Tmin are daily minimum and maximum temperatures respectively and LDT is the lower developmental threshold. If the daily mean temperature $Tmean = ((Tmax + Tmin)/2)$ is less than the lower developmental threshold, then Tmean is set equal to the lower developmental threshold LDT (McMaster and Wilhelm, 1997). Then we calculated the number of degrees per day, summed it up across time until we reached K_2. The number of days for each generation was then $d = K_2 / Sum(Tmean-LDT)$.

We could then estimate the number of successive generation that could be completed within a given year, using recorded temperatures from 1996 to 2013.Because we estimated K_2 for the first emerging beetle, the last and the median of emergence time we also determined the number of generations per year for early, late and median emerging beetles, giving a median estimate and its range of variation (e.g. confidence interval).

For estimating the number of generations each year we assumed that the first parental flights occurred when the maximum temperature (Tmax) was above the flight threshold required for the *I. sexdentatus*, i.e. 18C° (Chararas, 1962; Lieutier and Yart, 1989) for two days in a row.

2.5.3. Interactive effect of temperature, breeding substrate quality and quantity on the number of offspring and their individual fitness

The response variables were the total number of offspring per quarter bolt and their sex ratio, and the mean value of fresh weight and wing-load for the young adults emerged from a given quarter bolt.

The total number of offspring and the sex ratio is important to estimate population growth rate. Body weight is known to influence the fitness of bark beetles as in general large females have higher fat reserves and then disperse further, better survive extreme temperatures and lay more eggs compared to smaller ones; while larger males have better flying capacity and maximise their fitness by producing more aggregation pheromones (Amman and Cole. 1983). The wing-load or wing loading is calculated as the ratio of fresh body size to wing area and is a proxy for dispersal capacity (Byrne at al. 1988; Yao and Katagiri. 2011). Here the wing area was calculated as the product of elytra width by its length.

The explanatory variables included the mean temperature of the climatic chamber, phloem volume (phloem thickness × quarter bolt width × bolt length) as a proxy of food quantity, bark thickness as a proxy of temperature insulation and tree identity as a proxy of food quality (e.g. terpenic or phenolic content of the phloem). We tested together the effect of phloem volume and bark thickness since they were not correlated.

To test the effect of temperature and breeding substrate on the total number of offspring, we applied a generalised linear model (GLM) with the Poisson family for count data (with a log link function). Because we detected overdispersion, we corrected the standard errors using a glm quasipoisson with log link function (Zuur et al. 2009).

For the offspring traits (weight, wing load) we used linear regression (lm), while the sex ratio was modelled as proportional data with binomial family and logit function in order to linearize the response variable (R Development Core Team. 2012).

In all models, we applied a model simplification, by removing non-significant interactions through backward model selection or dropping non-significant variables one at time and repeating hypothesis testing. The significance of each explanatory variable was tested by comparing the deviances of the fitted model with and without the non-significant terms with Chi-square test for the glm and by anova for linear models (F-test) (Zuur et al, 2009). In order to meet the assumptions of normality and homogeneity of variance we checked the residuals of the linear models; significance of effect was based on α=0.05. The data analysis was performed in R (R Development Core Team. 2012).

3. Results

3.1. Lower developmental threshold for *Ips sexdentatus*

The brood development of *I. sexdentatus* was successful in five climatic chambers: 15°C, 18°C, 21°C, 23° and 25.5°C respectively, thereby their temperatures allowed complete adult beetle development. However, bolts reared at mean temperature of 12°C failed to achieve adult emergence, suggesting the presence of a limiting temperature threshold (Table 1). The number of offspring increased from 5 to 26 per female and the development time for half of the offspring population decreased from 121 days (ca. 17 weeks) to 35 days (5 weeks) with increasing mean temperature (from 15°C to 25.5°C) (Table 1).

Table 1. Summary table with development time and rate of development (1/d) for *Ips sexdentatus*

Tmean	*Sample size (nb quarter bolts)*	*Number of bolts with successful development*	*% development success*	*Total number of offspring / climatic room*	*Nb offspring / productive female (mean ± SE)*	*Development time (d) for the first offsping (mean ± SE)*	*Development time (d) for the median offsping (mean ± SE)*	*Development time (d) for the last offsping (mean ± SE)*
12 °C	18	0	0	0	0	-	-	-
15 °C	18	6	33%	70	5 ± 3	81 ± 6	121 ± 6	132 ± 6
18 °C	18	8	44%	101	21 ± 3	71 ± 5	93 ± 7	109 ± 7
21 °C	18	16	88%	351	12 ± 3	42 ± 1	50 ± 1	62 ± 2
23 °C	18	15	83%	388	26 ± 3	34 ± 1	40 ± 1	52 ± 1
25.5 °C	18	13	72%	311	24 ± 5	30 ± 1	35 ± 1	43 ± 1
Total	108	58		**1221**				

The development rate (1/d) linearly increased with increasing temperature within the studied range (15°C - 25.5°C). The regression equations of developmental rate versus the tested temperature regimes showed a very good fit to the data for first, median and late offspring emergence (Figure 1, Table 2).

Table 2. Summary table of results for the weighted least squares regression of development rate against mean temperature of climatic chambers

				1/d = a + b x Tmean	
OBSERVED OFFSPRING EMERGENCE	***N***	***R^2***	***P value***	***(-)a ± SE***	***b* ± SE**
FIRST OFFSPRING EMERGENCE	6	0.0965	<0.003	0.023 ± 0.006**	0.002 ± 0.0002***
MEDIAN OFFSPRING EMERGENCE	6	0.0972	<0.002	0.024 ± 0.005**	0.002 ± 0.0002***
LAST OFFSPRING EMERGENCE	6	0.0978	<0.001	0.018 ± 0.003**	0.002 ± 0.0001***
* < 0.05; **< 0.001; ***< 0.001					

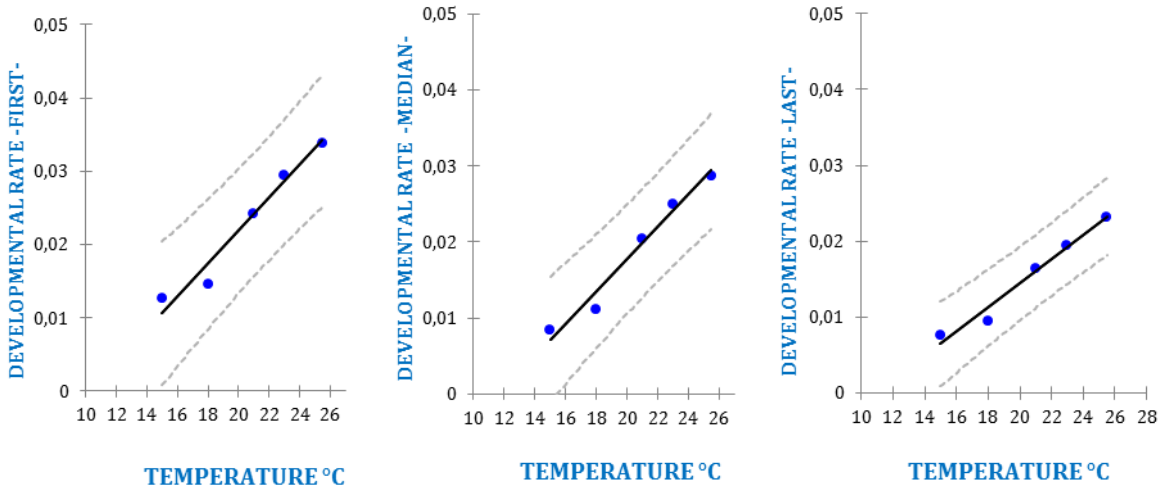


Figure 1. Relationships between mean temperatures (x-axis) and mean development rate per day (y-axis) of *I. sexdentatus* brood development, for the first, median and last emergence. The solid line represents the linear relationship between the temperature and developmental rate, while the dashed line represents the confidence intervals. The straight lines were fitted by using weighted least squares regression.

The intersection of the regression line with the x-axis (i.e. where the rate of development equals zero) gave the value of developmental thresholds (LDT± SE) for the first, median (50% of the population) and last brood emergence (Table 3). As shown in the table the lower developmental threshold was close to 11°C and the sum of degree-days required for complete development was between 450 and 650 on average. Overall the K1 method gave smaller sums of degree-days while the K2 and K3 methods produced very similar estimates (Table 3).

Table 3. Summary table with lower developmental threshold values (LDT) and thermal requirement (degree-days) K calculated with three different methods. K_1 estimated by the regression equation (K_1=1/b); K_2 calculated according to the law of total effective temperatures K_2 =d (T-LDT) and K_3 estimated by the sine wave method for first, median and last offspring emergence, respectively. Where: SE = standard error, K= thermal sum estimated in degree-days, T = programmed fluctuating temperature (°C), LDT = lower developmental thresholds in °C.

OBSERVED OFFSPRING EMERGENCE	*DEVELOPMENTAL THRESHOLD*	*THERMAL SUM 1* K_1 *=1/b*	*THERMAL SUM 2* K_2*=d(T-LDT)*	*THERMAL SUM 3 sine wave method*
	LDT ± SE	K1 ± SE	K2 ± SE	K3 ± SE
FIRST OFFSPRING EMERGENCE	10.3 ± 1.3	445 ± 22	453 ± 26	458 ± 25
MEDIAN OFFSPRING EMERGENCE	11.6 ± 1.1	474 ± 21	517 ± 52	523 ± 53
LAST OFFSPRING EMERGENCE	11.0 ± 1.0	625 ± 24	678 ± 59	663 ± 65

3.2. Estimation of population growth rate and prediction of number of generations/ year

The starting date for degree-day calculation was set when the recorded daily maximum temperature (Tmax) exceed (18°C) which corresponds to the flight threshold of I. sexdentatus (Chararas, 1962; Lévieux et al, 1985). During the 18 years study period the dates for first parental flight showed a high variation with almost one month difference; for instance in 2008 the dispersal flight begin on the 21th of February while in 2006 the flight conditions were

favorable from 25th of March, while the mean date along the whole study period would be around the first week of March (Appendix, Table 1-3)

For each year from 1996-2013 we predicted the total number of generation/ year (Figure 2) and the number of days required for the development for each generation (Figure 3). In general, during the 18 years study period the predicted number of generations varied from a minimum of one generation/year up to three generations/year. By using the mean sum of degree-days (517±52 DD) for 50% brood emergence, we could predict two generations per year from 1996 - 2013 without variations across the studied period. While using the predictions with the largest accumulated heat sum for the whole brood emergence or the last offspring emergence (678±64 DD) resulted only in one up to two generation/year, although in eight years out of the 18 years study period, the conditions were favorable for the full development and emergence of one generation only. Forecasting with the lowest heat sum required for the first offspring emergence (453±26 DD) yielded in three generation/year (Figure3). However, in four years (1996, 2002, 2007,2008 respectively) our model simulated only two-generations/ year (Figure 3, Appendix, Table 3).

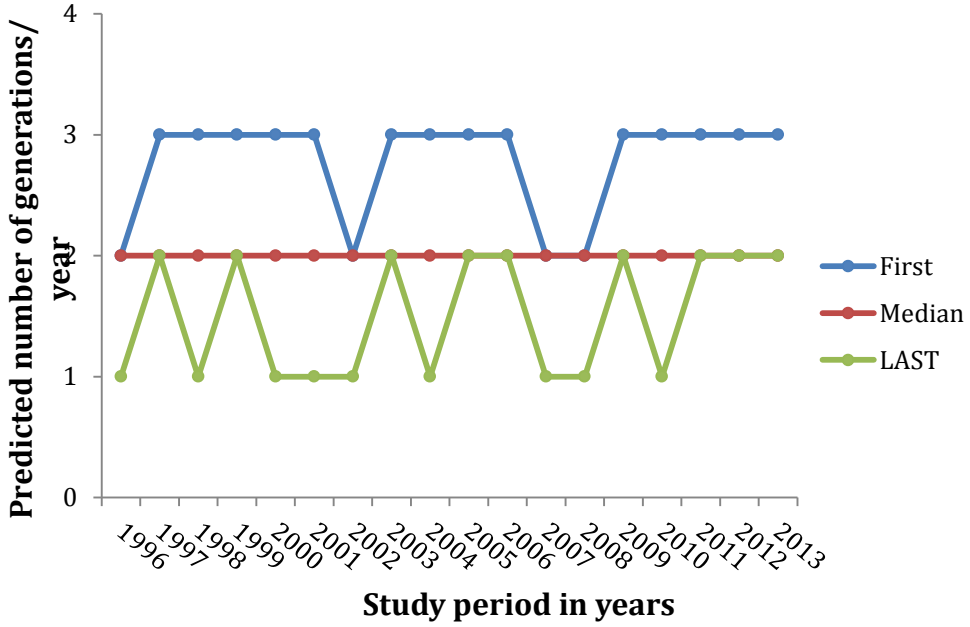


Figure 2. Predicted number of generations/year over the study period (1996-2013) based on estimated sum of degree- days (K2 method) and registered mean temperatures. The x-axis represents the study period in years, while the y-axis presents the predicted number of generations per year. Blue color stands for first offspring emergence; red color represents 50% (median) offspring emergence, while green color is the estimations for last offspring emergence.

The development time varied between generations. From parental flight (P) until the emergence of the first generation (F1) the median developmental time was on average 18 weeks (range 15 to 20 weeks), whereas for the second generation (F2) it was only 10 weeks (range from7 to 12 weeks). When there was a third generation (F3) full brood development it required 8 weeks (Figure 3). So on average the developmental time for first generation lasted from mid-March until end of June), in case of the second generation from end of June until mid-August, while the last generation developed from mid- August until the last week of October (Appendix, Table A)

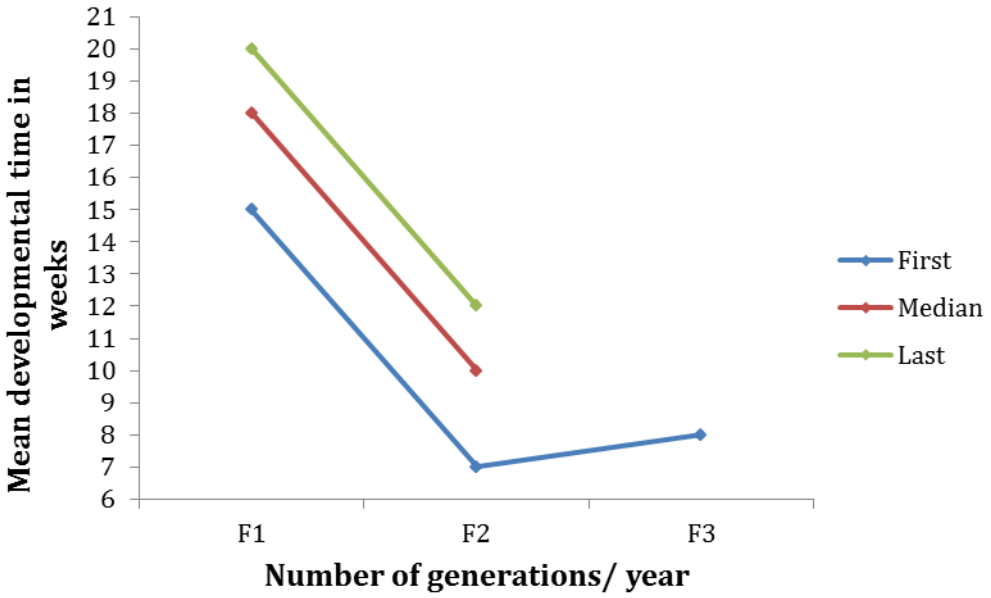


Figure 3. Mean number of weeks required for development of the different generations/ year; x- axis represents the generation rank (F1- F3) predicted for the study period (1996-2013), while the y-axis is the calculated mean developmental time in weeks. Blue color stands for first offspring emergence, red=median offspring emergence and green = last offspring emergence

3.3. Interactive effect of temperature and breading substrate characteristics on total number of offspring and their fitness.

The final dataset had 90 observations out of which 33 observations were zero counts due to mating failure or female sterility or other reasons that we were unable to observe. Therefore we modeled the dataset in two steps. First, we included all observations including the zero counts and applied a simple logistic regression; for the second step we kept only the observations that were non zeros and modelled them using a Poisson regression. Here we present the model results without zero and NA observations.

Table 4. Summary table with results of generalized linear model and linear models for the effect of temperature and breeding substrate on population **(a)** and individual **(b)** - level characteristics of offspring. Significant values are highlighted in bold (***P < 0,001; **P < 0,01; *P < 0,05)

a) Population level response variables

		RESPONSE VARIABLES			
EXPLANATORY VARIABLES	**DEGREES OF FREEDOM**	**TOTAL NUMBER OF OFFSPRINGS**		**SEX RATIO**	
		Estimate ± SE	***P value***	**Estimate ± SE**	***P value***
TEMPERATURE	1	0.066360 ± 0.026666	**0.00297****	(-) 0.001711 ± 0.010762	0.5698
PHLOEM VOLUME	1	0.000741 ± 0.006027	**0.04331***	0.006692 ± 0.002726	0.28783
BARK THICKNESS	1	0.670211 ± 0.069212	0.52333	(-) 0.262116 ± 0.311811	0.35064
TREE 1		0.650481 ± 0.814021		0.006189 ± 0.357706	
TREE 2	2	0.473638 ± 0.357178	0.42171	(-) 0.323520 ± 0.152329	0.05128
TREE 3		0.378689 ± 0.326831		(-) 0.334127 ± 0.133521	

b) Individual level response variables

EXPLANATORY VARIABLES	DEGREES OF FREEDOM	RESPONSE VARIABLES: MEAN WEIGTH		WING LOAD	
		Estimate ± SE	*P value*	Estimate ± SE	*P value*
TEMPERATURE	1	(-)0.000134 ± 0.000108	0.3043	(-)0.008797 ± 0.014433	0.7174
PHLOEM VOLUME	1	(-)0.000041 ± 0.000028	0.2574	0.002642 ± 0.003796	0.2852
BARK THICKNESS	1	0.004125 ± 0.003295	0.3576	0.333790 ± 0.436832	0.3658
TREE 1		0.021800 ± 0.003610		2.262548 ± 0.481391	
TREE 2	2	(-)0.000109 ± 0.001584	0.7653	(-)0.026390 ± 0.210073	0.9589
TREE 3		(-)0.000684 ± 0.001426		0.009387 ± 0.189040	

Climatic chamber temperature and phloem volume had a significant effect on the total number of offspring per female, with no interaction, which suggests additive effects. Bark thickness and tree identity had no significant effect on the number of offspring (Table 4a).

The total number of offspring per female significantly and exponentially increased with increasing temperatures with no apparent asymptotic effect (Figure 4), and also with higher volume of phloem.

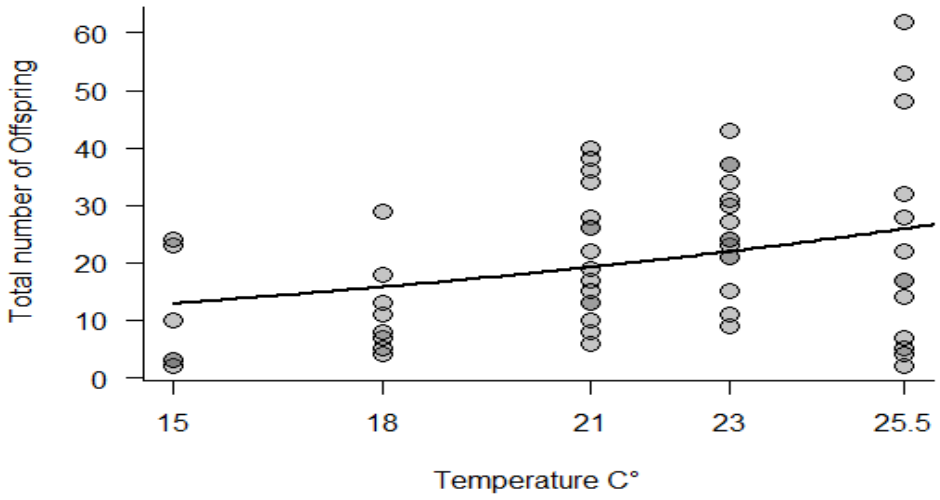


Figure 4. Effect of mean temperature on the total number of offspring per female

By contrast, none of the explanatory variables had any effect on the sex ratio of offspring (Table 4a, Figure 5). The sex ratio therefore remained constant and equal to ca. 1:1 (50% of males).

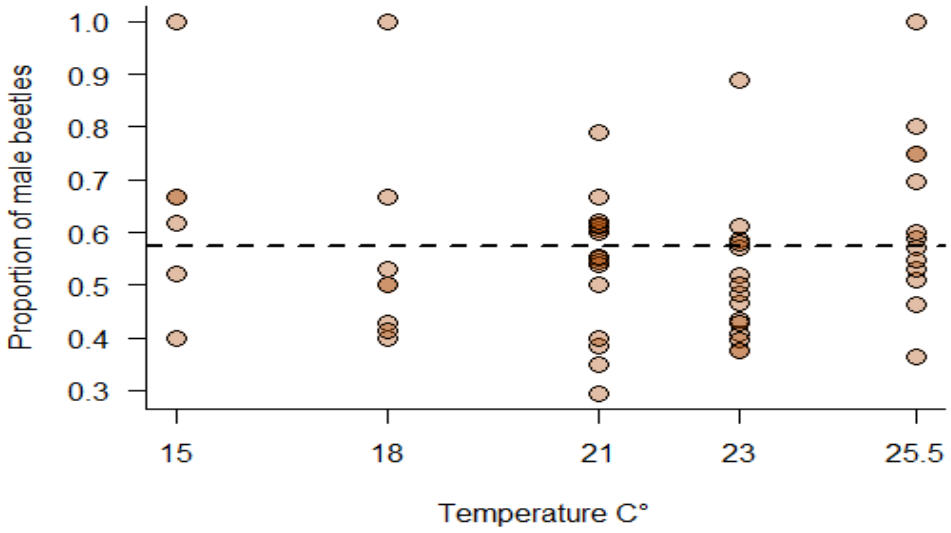


Figure 5. Effect of mean temperature on the sex-ratio of offspring.

None of the explanatory variables had any significant effect on the mean individual characteristics of young emerging adults (Table 4b) (Figure 6 & 7). The mean fresh weight was consistently close to 20mg regardless of the temperature of development and the wing load equal to ca 2.5mm^2/g.

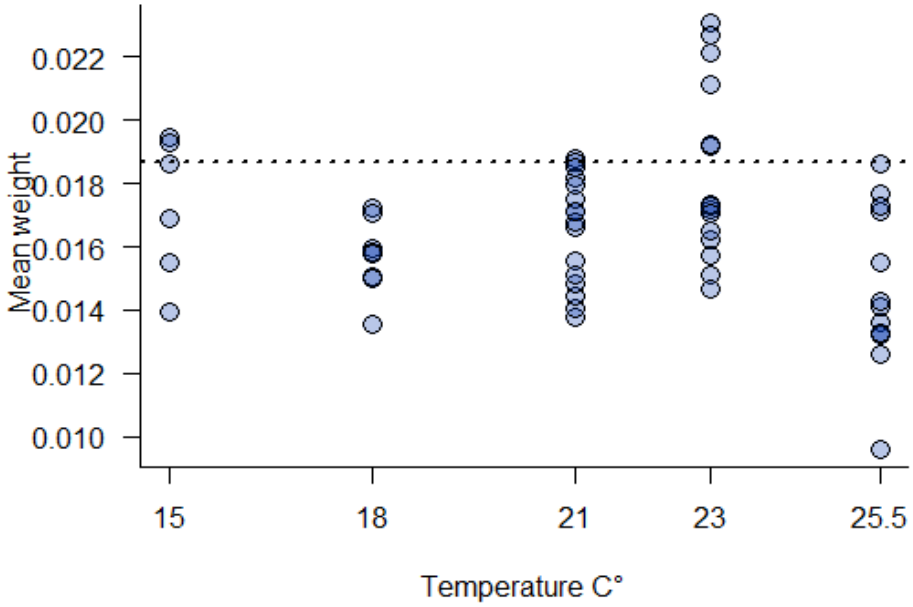


Figure 6. Effect of mean temperature on the mean fresh weight (g) of offspring.

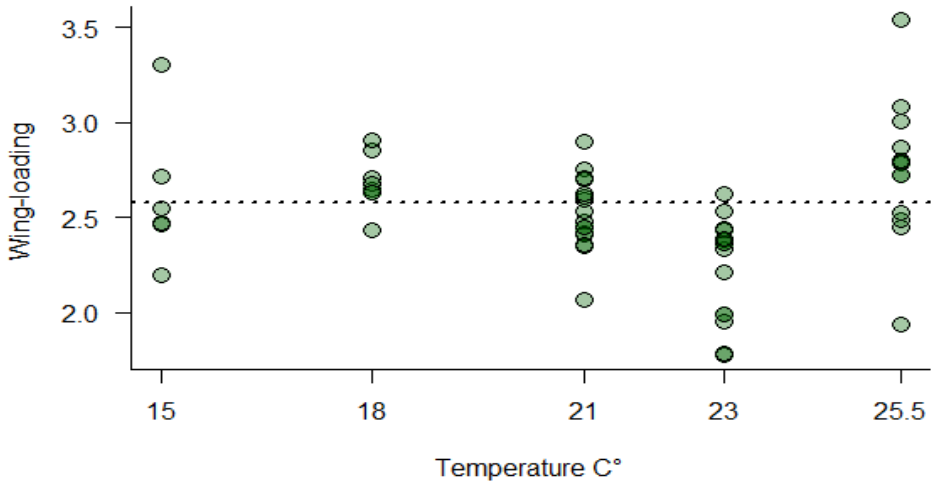


Figure 7. Effect of mean temperature on the wing-load (cm²/mg) of offspring

4. Discussion

4.1. Lower developmental temperature threshold for *Ips sexdentatus*

To our knowledge this study represents the first attempt ever to identify a lower developmental threshold value and quantify thermal requirements for *I. sexdentatus,* although it is considered the most damaging bark beetle species in southern Europe (Etxebeste 2012).

The minimum temperature for development was estimated at ca. 11 ± 1 °C, with very small differences between the estimates for the development of first (10.3), last (11.0) and medium (11.6) emerging adults. These values are on the same order of magnitude, although higher, than for the most common bark beetle species in Europe, *Ips typographus,* which need at least 8.3°C to develop (Wermelinger and Seifert, 1998). For other bark beetles from boreal areas, minimum required temperatures were also quite low, like 5 °C for *Dendroctonus rufipennis* in Alaska (Werner and Holsten, 1984), around 4°C for *Tomicus piniperda* in northern Finland (Saarenmaa 1985) and 4.5 °C to 5.5°C for the Mountain pine beetle *Dendroctonus ponderosae* in Canada (Reid and Gates, 1970; Reid 1962 reported in Carroll et al. 2003). By contrast this threshold was found at higher temperature, i.e. 12.2 °C, for the woodborer *Monochamus galloprovicialis* (Coleoptera: Cerambycidae) in Portugal (Naves and Sousa. 2009). There are similar variations within a given species, for example the Scandinavian spruce bark beetle populations have a lower developmental threshold i.e. 5°C (Annila, 1969 cited by Wermelinger and Seifert 1998), than those from central European populations, with value varying between 7°C and 12°C (Netherer and Pennerstofer 2000, reported by Dolezal and Sehnal, 2007). This suggests an adaptation to climatic conditions, with species or ecotypes developing at lower temperatures in colder conditions. To confirm this hypothesis, it would be interesting to compare the minimum threshold temperature of development in populations of *I. sexdentatus* originating from different parts of its range, e.g. northern vs. southern Europe.

Furthermore, beetle development life stages have different thermal thresholds values (Bentz et al. 1991). For example, Wermelinger and Seifert (1998) observed that in *I. typographus* the egg stage requires the highest threshold value (10.6°C) while maturation feeding can occur at 3.2°C. Our experimental approach did not allow making such comparison between life stages

in *I. sexdentatus* because we were mainly interested in the number and fitness of offspring (young adults) and then kept them developing until emergence. We would have had to produce more rearing bolts and remove them earlier from the climatic chambers to know about the number of eggs laid or alive larvae for example, after removing the bark. Nevertheless other techniques, like the "sandwich method" which consist in putting a phloem layer between two glass layers, make it possible to monitor the development of several developmental stages in a non destructive way. This could be used for *I. sexdentatus* in order to better identify which life stages are more sensitive to low temperatures.

We used simple linear regressions to calculate minimum developmental temperature thresholds. It is the most common method applied to estimate these threshold values for insect development over a restricted temperature range (Campbell et al. 1974). The main advantages of the linear model are its simplicity and accuracy (Wermelinger and Seifert, 1998). Here we found very consistent values for the three linear models developed for early, medium and late emerging beetles, which is a way to test for the reproducibility of the method.

However, in natural conditions insect development often do not follow a linear relationship especially because the developmental rate may decrease after a second threshold at high temperatures (McMaster and Wilhelm, 1997; Damos and Savopoulou, 2011). We did not observe such decrease in developmental within the tested range of temperatures so were unable to identify an optimal temperature. Further investigations would be needed to test the effect of temperatures higher than 25.5°C to estimate this optimal threshold value (Campbell et al.1974) which might also help to better predict the effect of global warming. There are available nonlinear models that can be applied to predict the developmental rates over such a large range of temperature regimes, like the polynomial model, Logan-Lactin model or complex biophysical models (Damos and Savopoulou, 2011).

4.2. Sum of degree- days for the complete development of *Ips sexdentatus*

The number of degree-days for the complete development of 50% of the offspring was estimated at 517 ± 52 DD by the averaging method. It ranged from 453 DD for the first emergence to 678 DD for the last adult beetle emergence.

We use two other methods to calculate the heat sums, i.e. sums of degree-days. The sine wave method gave very consistent results (only 6 DD of difference for the median offspring emergence). This due to the fact that the sine wave method is based on theoretical models using sinusoidal fluctuations of temperatures while we also programmed temperature regimes in our climatic chambers on the basis of sinusoidal daily fluctuation. The linear regression method, using the reciprocal of the slope (1/b), is known to be less accurate because it doesn't take into account daily temperatures variations (Campbell et al. 1974, Wermelinger and Seifert, 1998). In our case it would have predicted 8% lower values of sum of degree-days.

To our knowledge there are no available studies about the thermal sums required for complete adult development of *I. sexdentatus*. For *I.typographus* in Finland the median thermal sum needed for complete development varies within the range of 625- 750 degree days above the developmental threshold (LDT) of 5°C (Annila, 1969 cited by Jönsson et al. 2007) while in Central Europe the median heats sum equals 572 degree days with LDT= 8.3°C (Wermelinger and Seifert, 1998).

Translated into number of days for adult development at constant temperature, these sum DD estimate indicate that *I. sexdentatus* required from 35 days at Tmean=26.5 °C up to 121 days at Tmean=15 °C. This clearly demonstrates that as for other insects in general and bark beetles in particular, the developmental time is highly temperature dependent.

Our observations are comparable with that of older studies on the same species. Chararas (1962) reported that in natural conditions the development time from egg to adult stage can be up to 78 days under controlled laboratory conditions, while with constant temperature (20-21°C) is only 43 days, which is comparable to with our observation of 42days at Tmean=21 °C. According to Vallet (1981, cited by Lévieux et al 1985), the beetle can complete its development in 23 - 24 days, which is close to 30 days, the number of days before the first offspring emergence at Tmean = 25.5°C in our experiment. However the authors of that study did not provide information about ambient temperatures.

For *I.typographus* the reported *"*mean time of swarming" at constant temperature of 20°C was 51 days (Dolezal and Sehnal. 2007) which is very close to our estimated value of 50 days for *I. sexdentatus* at Tmean=21°C. North American studies on the mountain pine beetle (*D. ponderosae*) populations observed 30 days from egg to adult development at a constant 24°C temperature (Safranyik and Whitney cited by Bentz et al, 1991), while a phenology model by Bentz et al (1991), estimated that 28 days are required for the adult stage development (50 % emergence) at 24 °C temperature. It is remarkable to notice that for similar average temperatures (20-25°C) many bark beetle species take similar time to develop a new generation, i.e. one to two months.

Many studies have demonstrated that the developmental time of bark beetles highly influenced by environmental conditions especially by temperature (Seidl et el. 2007; Baier et al. 2007, Jönssoon et al. 2007, Wermelinger and Seifert, 1998; Marini et al. 2012). From a biological point of view poikilothermic organisms are adapted to particular temperature ranges; therefore temperature plays an important role in their biological cycle, influences their developmental rate and defines their distribution (Logan et al. 2003). According to the literature, the effect of temperature on poikilothermic organisms is due to enzymatic reactions, which controls their metabolism, for instance "*the conformation of enzymes is essential step in the enzymatic reaction and this conformation depends on temperature which exert catalytic effect at molecular levels*" (Laudien, 1973 cited by Damos and Savopoulou, 2011). It is recognized that insects' enzymes activity would be negligible at temperature lower than 10°C and maximum at 35-45°C (Evans and Payne 1964, cited in Douglas 2013). Warm temperatures would then trigger higher activity of enzymes involved in digestion (Douglas 2013) allowing a better conversion of feeding resources into cellular multiplication and growth and then accelerated ontogenic development.

4.3. Effects of temperature on population growth rate and individuals' fitness

4.3.1. Voltinism

Increased developmental rate can lead to increased voltinism, i.e. higher number of generations per year, in multivoltine species like bark beetles (Wermelinger 2004; Jönsson et al. 2007; Klapwijk et al. 2012). We used our degree-days model to reconstruct the theoretical number of *I. sexdentatus* generations that occurred in the past 17 years in Aquitaine. According to the recorded temperatures, there were on average two complete generations/ year with a partial and sometimes complete additional third generation. The developmental time for the first generation was around 18 weeks while the second generation took only 10 weeks to develop. Most of the time, the third generation could not fully develop due to low temperatures in fall (from October on). However it is known that if the last generation is not able to finish its development before ambient temperature falls below LDT (11°C) then beetles can hibernate and complete their development in the next spring (Chararas, 1962). Late instar larvae or pupae are known to be less sensitive to winter temperatures than eggs and young larvae in *I. sexdentatus* (Lévieux et al. 1985; Chararas, 1962).

Our estimation of 2-3 generations/year in southwestern France is comparable to the literature since most of the studies reported that normally in Central and Northern Europe *I. sexdentatus* is bivoltine (2 generations/ year) (Schwenke, 1974). At lower altitudes and then warmer climates it can exhibit three generations / year whereas in the Mediterranean region the beetle could develop 4 to 6 generations (Chararas, 1962, Schwenke, 1974).

4.3.2. Number of offspring per generation

Our study also showed that higher temperature regimes positively influenced the total number of offspring. The number of young adults produced per female varied from 5 at 15°C to ca. 26 at 25°C. Our statistical model showed that the increase in offspring number with temperature followed a linear relationship with no obvious asymptote. This means again that we did not reach the optimal temperature in the range we tested that further rearing trials at temperature above 25°C are needed to identify upper temperature threshold.

To our knowledge, there are no other published papers on the population productivity for *I. sexdentatus*. In a similar lab experiment with *I. typographus* (reared on logs, with a bark surface of 300 cm², one female/log) the number of offspring per female was about 20 (Anderbrant et al. 1985). However it is difficult to make comparison with other studies on the population growth rate in bark beetles because many other factors can affect the number of alive offspring per female, such as the amount of food resource which itself depend on the volume of phloem (Chararas, 1962, Bentz et al. 1991) and the density of parent beetles (i.e. intraspecific competition). In our experiment we did observe a positive effect of the volume of phloem on the number of offspring regardless of the temperature, indicating an additive effect of the two factors (no synergy nor antagonism). Breeding substrate quality, especially variation among individual trees or tree species (Amman, 1972; Erbilgin et al. 2013) can have a major influence on rate of insect development, notably through concentration in secondary metabolites which are known to be toxic for bark beetles larvae (Lieutier, 2004). We could not confirm this effect in our experiment as we did not found any "tree identity" effect on the number of offspring. However differences in phloem quality between the three maritime pine trees cut in the same stand might have been too small to detect their influence.

4.3.3. Sex ratio in the cohort of young emerging adults

We observed a sex ratio close to 1:1 in our experiment, which is comparable with the available literature on this species (Jactel, 1991), although Chararas (1962) reported a female skewed sex ratio (1:3,1:4) towards the dominance of females. In the similar study made by Anderbrant et al. (1985) on *I. typographus* they found a 1:2 sex ratio, which is consistent with the fact that these beetles species are polygamous. The observation that the sex ratio was balanced in the lab experiments (this study and Jactel et al. 1991) may be explained by differential mortality rate following emergence in the wild. Pioneers beetles initiating attacks on living trees are males, which means that they might be more exposed to mortality factors such as predation or preformed defence reactions in tree than females.

Anyway the more important result here is that temperature of development had no significant effect on sex ratio. Wermelinger and Seifert (1999) found no significant difference either in sex ratio for *I. typographus* offspring obtained at 20 to 30°C. This means that males and females probably have the sensitivity to temperature during their ontogenic development.

4.3.5. Young adults' individual fitness

Beyond the size of a population, the "quality" of the population is also important for explaining outbreaks. Thomson and Sahota (1981) defined population quality by the reproductive efficiency and survival capacity of the individuals that comprises this

population. Usually two main characteristics are measured in individuals as proxies of their reproductive and survival capacity, namely their size (or weight, which are often correlated) and dispersal ability (Anderbrant and Schlyter 1989) which we estimated through the wind load. For example Anderbrant et al. (1985) showed that "light" bark beetles produced fewer offspring than "heavy" ones. The fat content is also important as it indicates the amount of energy available for reproductive and dispersal functions (Byrne at al. 1988; Yao and Katagiri. 2011). We had planned to estimate the amount of lipid in offspring but due to time shortage this will be done later on.

When comparing offspring "quality" between climatic chambers we found not a single significant effect of temperature on either fresh weight or wing load although these life traits did vary (i.e. fresh weight varied from 0.010 to 0.026g and wing-load varied from 1.8 to 3.5 $mm^2.g^{-1}$). This means that temperature had an effect on the quantity but not on the quality of offspring. In a review paper, Anderbrant and Schlyter (1989) suggested that the main driver of bark beetles quality is intra-specific competition during larval development. The second most important factor of influence would be phloem quality but they do not mention any clear effect of temperature on beetle quality.

4.4. Practical applications

4.4.1. Understand and predict the population dynamics of *Ips sexdentatus*

The outcomes of this study can have important implication for the improvement of our understanding, and then prediction, of the population dynamics of *I. sexdentatus* within the frame of climate change. According to our laboratory experiment increasing temperatures have positive effects on the developmental rate (resulting in more generations per year) and population growth rate (number of offspring per female) and no detrimental effects on the sex ratio and individual fitness of the young, emerging adults. All in all, this means that populations may build up faster under warmer climate thus resulting in higher risk of outbreaks. Most of studies that address the question with bark beetles conclude that they are much likely to develop more frequent and severe outbreaks under warmer climatic conditions (Schwenke, 1974; Lévieux, 1985; Seidl et al. 2007; Logan et al. 2003; Wermelinger, 2004; Faccoli, 2009).

Let's take a simple example to illustrate this: in Aquitaine region, 2002 was one the coldest year during the 1996 - 2013 period with a mean temperature of 13°C. The first generation of *I. sexdentatus* developed in 105 days (1^{st} emergence) at 15°C on average so with a productivity of ca. 6 adults per female and then 3 "daughters". The second generation developed in 55 days at 19°C on average so producing ca. 16 offspring per female, i.e. 8 "daughters". There was not a third generation. In total in 2002 one adult female would have then produced: $3 \times 8 = 24$ young females.

The next year (2003) was the warmest year of the period with a mean temperature of 14°C. That particular year three generations of *I. sexdentatus* were produced. The first developed in 96 days at 15°C with a brood production of 6 offspring, i.e. 3 young females. The second developed in 43 days at 21°C with a production of 21 offspring i.e. ca 10 young females; and the third in 35 days at 23°C producing 26 offspring, i.e. ca. 13 young females. So in that year one female parent would have produced: $3 \times 10 \times 13 = 390$ young females. This shows that an increase in 1°C on average resulted in 390/24=16 times more young female adults.

Of course this is just one small part of a modeling exercise. Many other factors can play a role in bark beetle population dynamics under climate change, through both direct and indirect effects on population growth. In particular increased temperatures or drought are likely to reduce tree resistance to bark beetles attacks and development (Christiansen et al. 1987;

Koricheva and Larsson, 1998; Rouault et al. 2006; Jactel et al. 2012). Change in temperature may also modify the top-down regulation of insect herbivores by their natural enemies like predators and parasitoids (Rouault et al. 2006; Péré et al. 2013).

4.4.2. Bark beetle risk management after storm damage

After the recent two storms that hit the Aquitaine forest in 1999 and 2009 a systematical outbreak of *I. sexdentatus* was observed on following years. The main reason for this epidemic response was that a huge amount of breeding substrate for bark beetles was provided by the wind throw. Not only broken trees were more prone to bark beetles attacks but also the many large piles of cut logs that were stored along forest roads and on which *I. sexdentatus* could reproduce, build up into epidemic populations and then attack standing living trees in neighbouring stands (Rossi et al. 2009). To circumvent this problem, insecticides were sprayed to piles of cut logs; however, this was made at very high financial cost (subsidized by the French government and Aquitaine region) and unknown environmental cost for local biodiversity. Alternative options are therefore desirable. Here we suggest that one could reduce the use of pesticide by identifying the piles of logs that really need to be treated. If logs are removed and sent to pulp or saw mills before bark beetle offspring emerge they don't represent any danger for nearby forest stands. So the idea is to use the results of the study to predict the development time of bark beetles in piles of logs according to the date of attack by the parents (easy to detect using the presence of frass on the bark of logs) and to the ongoing temperatures. A software could be developed to indicate every week at which point a population of larvae is developing in a given pile of logs and then send a warning message to forest managers to urge the removing of the pile if young beetles are about to emerge.

5. Further research

The results of the study contribute to a better understanding of the phenology of *I. sexdentatus*, however we have identified new research areas that could be addressed in further studies.

First of all, would be important to finalize the dataset (estimate the fat content of individual offspring) and to complete analysis of temperature effects on population "quality". Secondly, it would be interesting to expand our retrospective analysis of the number of *I. sexdentatus* generations per year in Aquitaine with a similar theoretical study on the mean number of generations per year in other, more contrasting regions, like in northern (Germany) vs. southern (Greece) European countries, based on their mean passed temperatures. Thirdly additional breeding trials could be set up in order to determine the optimal temperature and the upper developmental threshold, which may hinder beetles development. This would help to parameterize a simulation model for predicting population growth rate under climate change.

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Appendix

Table A. Developmental time (in weeks) for the predicted number of generations over the study period (1996-2013). Where first emergence= predictions with 453 degree- days, median or 50% emergence= predictions with 517 degree- days, last emergence= predictions with 678 degree- days; while F1, F2, F3 = the predicted generations/ year

Years	Tmean	Parental flight- P	*FIRST EMERGENCE*			*MEDIAN EMERGENCE*		*LAST EMERGENCE*	
			F1	F2	F3	F1	F2	F1	F2
1996	13.09	22-Mar	13	7	-	17	12	18	-
1997	13.20	28-Feb	16	8	7	20	8	21	11
1998	12.30	13-Feb	19	7	10	22	9	24	-
1999	12.82	09-Mar	14	7	7	18	8	19	13
2000	12.80	08-Mar	15	7	10	19	10	20	-
2001	12.57	06-Mar	16	7	9	19	10	21	-
2002	13.07	12-Mar	15	8	-	19	13	20	-
2003	13.99	09-Mar	14	6	5	16	7	18	9
2004	12.07	02-Feb	21	7	8	24	8	25	-
2005	12.40	15-Mar	14	6	8	15	9	17	13
2006	13.29	25-Mar	12	5	7	15	8	16	11
2007	12.46	13-Mar	13	8	-	17	12	18	-
2008	12.37	20-Feb	18	7	-	21	13	23	-
2009	12.98	12-Mar	15	7	8	18	9	19	14
2010	12.03	17-Mar	14	7	8	17	10	18	-
2011	13.79	14-Mar	12	8	7	16	9	17	11
2012	12.70	29/02	16	7	8	17	8	21	13
2013	12.62	07-Mar	18	6	9	20	10	20	13
		MEAN	15.3	7	8	18.3	10	20	12
		SE	0.56	0.18	0.3	0.56	0.42	0.56	0.35



Photo1. Tree cutting, selecting the breeding material



Photo 2. Cutting the logs along in four radial sections



Photo 3. Measuring bolt features and labelling prior waxing



Photo 4. Drilling the holes through the bark surface on the phloem



Photo 5. Inoculated bolts with male insects, covered with transparent capsule



Photo 6. Successful beetle installation indicated by the presence of frass



Photo 7. Insect mating- inoculation of female beetles



Photo 8.Successful mating



Photo 9. Inoculated bolts with transparent collectors on which the log characteristics and female number were noted



Photo 10.Bolts in mesh bags with the transparent collectors



Photo 10. Logs transferred into the climatic chamber



Photo 11. Programmed Friocell climatic chamber





Photo 10. Individual insect labeling and measurements of offspring fitness traits

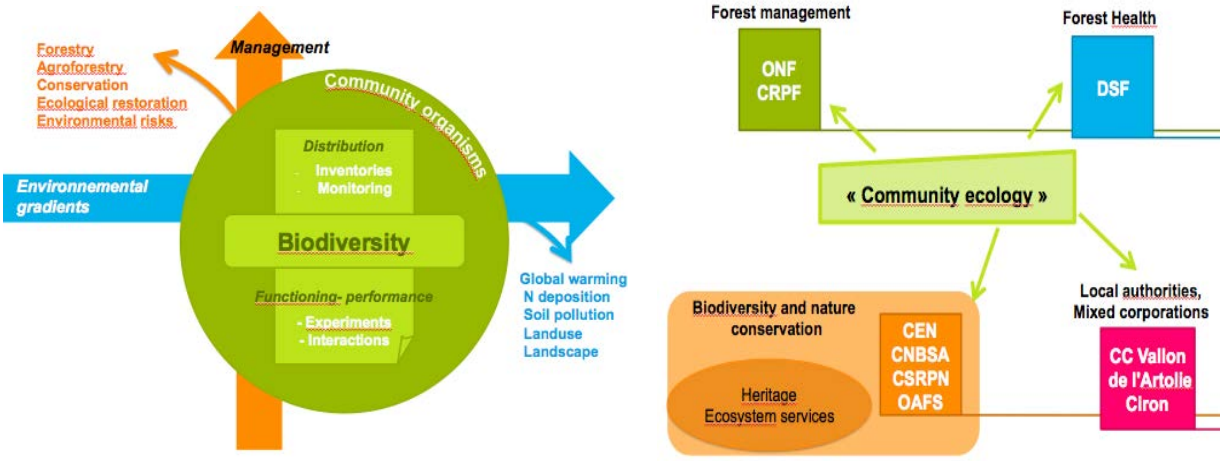
General presentation about the host institute - INRA BIOGECO-

The National Institute for Agricultural Research (INRA) is the second largest research institute in France and provides scientific knowledge on economic and social innovations in areas of food agriculture and the environment. Personally I had the opportunity to complete my internship period and Masters thesis work at UMR INRA BIOGECO- located at Pierroton (Aquitaine region).

The research program of the Joint Research Unit for "Biodiversity, Genes and Communities" is directed towards the analysis of mechanisms governing the evolution of diversity at different levels (communities, species, populations, genes) with a view to sustainable management of resources and environments. Research activities intend to promote a more integrated analysis of biological diversity, by considering interactions between species, populations and individuals as drivers of its evolution.

The Community Ecology team focuses its research area on species assemblages (trees and animals), and their interactions in relation to environmental change. They study ecological and evolutionary processes, which are responsible for the maintenance of biodiversity in ecological communities. The research develops through modeling approaches, experimental and empirical studies in a range of extensive habitats ranging from wetland forest to grassland communities mainly in Aquitaine region. The main research topics include: (1) the functional ecology and the role of biodiversity, (2) effects of tree species diversity and resistance of plantation forests to forest insect pests at different spatial scales, (3) functional role of insectivorous birds in forest insect predation, (4) studies on the functional role of landscape heterogeneity on the population levels of the pine processionary moth, evaluating and searching for biological control measures of maritime pine-bug in Corsica, (5) and phytoremediation of contained soils and waters by trace elements. They work in close cooperation with other research institutes, governmental and public organizations Additionally, the team is actively involved in international research projects such as the GREENLAND projects and local projects supported by the regional council of Aquitaine region.

Community Ecology Team research scheme and its cooperation's with other research institutes, governmental and public organizations.



Abstract

Global warming may trigger higher risk of biotic damage in forests because pest insects can quickly respond to increasing temperature through improved reproductive success. The present study aimed at studying the effect of warmer conditions on the population dynamics of *Ips sexdentatus*, the stenographer bark beetle. We performed breeding trials at six temperature regimes to determine the thermal requirements for complete development and we developed a model of degree-days to estimate the voltinism of the insect. We also tested the effects of temperature and breeding substrate on the number of offspring and their individual fitness. The minimum temperature threshold for *I. sexdentatus* development was estimated at 11±1°C, and the sum of degree-days at 517±52 DD. Adult developmental time required from 35 days at 25.5°C to 121 days at 15°C. On average, *I. sexdentatus* had two complete generations per year in Southern France over the past 17 years. The number of offspring per female exponentially increased with increasing temperature and volume of phloem whereas these variables had no influence on the sex ratio and individual beetle's fitness. This suggests that increasing temperatures would result in more generations per year and more offspring per generation and in consequence higher risk of bark beetle outbreaks.

Resumé

Le réchauffement climatique menace particulièrement les forêts, peu aptes à s'adapter à des changements rapides. La reproduction des ravageurs forestiers est au contraire favorisée par ces nouvelles conditions, augmentant ainsi le risque d'épidémie. Cette étude a cherché à déterminer les besoins thermiques et le temps de développement de *Ips sexdentatus* sous six différents régimes de températures testés en laboratoire. Nous avons aussi étudié le voltinisme de cette espèce ainsi que les effets de la température et du substrat sur les caractéristiques des descendants. Le seuil de développement a été estimé à 11±1°C et la somme de degrés/jours pour l'émergence des descendants à 517±52 DD. Le développement jusqu'à l'état adulte demande de 35 jours sous une température de 25.5°C à 121 jours à température de 15°C. Nous pouvons ainsi estimer que *I. sexdentatus* a présenté deux générations complètes par an en Aquitaine lors des 17 années passées. Les températures élevées ont pour effet d'augmenter le nombre d'individus par descendance sans toutefois avoir d'incidence sur le sex-ratio ni sur la taille moyenne ou la charge alaire des jeunes adultes. Ces résultats suggèrent qu'un accroissement des températures augmenterait le nombre de générations par an et le nombre d'individus par génération, contribuant à augmenter fortement le risque de pullulations.