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Abstract

In the Toba Highlands of North Sumatra (Indonesia), coffee production (*Coffea arabica* L. var. *Sigarar Utang*) is an important outcome for smallholders; however, the attack of the coffee berry borer (CBB) *Hypothenemus hampei*, is an obstacle for the development of coffee cultivation in this area. This pest causes great economic losses produced by the development of its offspring inside the coffee berries, making it difficult to control. This concerning situation has led us to consider the development of a CBB control strategy, but beforehand, it was necessary to acquire key information on the phenology of the coffee tree and its implication on the bioecology of the pest. Thus, two study designs were set up, one comprising six plots with two different age classes and the other corresponding to a single plot dedicated only to the study of short distance dispersal of CBB. Part of this study focused on the phenology of the coffee trees and showed that berry production mainly takes place in the upper parts of the trees and significantly decreases with tree age. Due to the equatorial climate, berries were practically always present. Berries were produced following two major flowering periods and some minor ones distributed over the year, and harvested at regular intervals. Berry distribution on the branches varied over time. Dynamics of infestations by CBB showed that ripe berries were more infested than unripe berries because they had been exposed longer to CBB attacks, that older trees were more exposed than younger trees and that infestation was evenly distributed along branches. In addition, internode pedestrian dispersal of CBBs was shown to occur, but considerably less frequently than airborne dispersal. In conclusion, it appears that in the agro-climatic context of the Toba region, the virtual year-round presence of berries - which fosters CBB infestations and CBB short-distance dispersal - is a constraint that must be taken into consideration for designing

future pest management measures. To this end, it will be necessary in particular to evaluate the potential of trapping mainly used in tropical areas and to put into practice the sanitation harvesting applied in other countries.

Key words: coffee tree, fruiting, climate, coffee berry borer, dispersal, Toba Highands.

1. Introduction

The Sumatra archipelago is the main coffee-producing area in Indonesia. Its geographical diversity makes it possible to grow robusta coffee trees (*Coffea canephora* Pierre var. robusta) in the lowlands and Arabian coffee trees (*Coffea arabica* L.) on the high-elevation plateaus, in particular in the province of North Sumatra.

In the Simalungun district of North Sumatra, the dominant *C. arabica* variety is *Sigarar Utang*, mainly cultivated unshaded, around Lake Toba. This coffee, originating from a natural cross between the Tim Tim cultivar and a lineage of the Bourbon variety, belongs to the internationally-famous Mandheling Coffee group (Mawardi, 2008, 2009). The Indonesian Coffee and Cocoa Research Institute (ICCRI) introduced this variety in the 1980s as an alternative to *robusta* cultivation. It is higher yielding than the Sumatra typical variety, which was once grown in the area, but it is described as moderately resistant to leaf rust caused by *Hemilea vastatrix* Berk. & Br and susceptible to the coffee berry borer (CBB) *Hypothenemus hampei* (Ferrari) Coleoptera: Curculionidae: Scolytinae), the major coffee pest worldwide (Hulupi & Nugroho, 2013). Since the introduction of *C. arabica* in this district, productivity has remained fairly low, at approximately 50 or 65% only of its full potential (Saragih, 2013). According to Saragih (2017), all coffee plantations are grown by smallholders and are said to be poorly managed due to lack of training and to agroecological shortcomings (Dufour *et al.*, 2019). This unfavourable context for high productivity is made even worse by damage caused by the CBB reported by several authors (Mawardi & Wiryadiputra, 2009; Saragih, 2013). Indeed, by digging galleries inside the coffee beans to complete its life cycle, the CBB makes them unfit for consumption (Vega *et al.*, 2015). Thus, before being marketed, coffee must be sorted in order to eliminate CBB-damaged beans that are among the defective forms to be discarded.

In Indonesia, CBB was first detected in Java in 1909 (Cramer, 1957) then in Sumatra in 1918 (Corporaal, 1921) before spreading to other islands and colonising all the coffee production areas. More recently, significant attacks by CBB were reported on *C. arabica* in North Sumatra. Monthly data from the district of Simalungun from May 2018 to September 2019 revealed a high percentage of holed berries, ranging from 32 to 58% (I W. Kerana, unpublished).

Face of this concerning sanitary situation, it was considered crucial to develop an efficient and sustainable strategy to control the pest and curb the infestation to acceptable levels in order to reduce harvest losses and shorten sorting operations, which heavily affect post-harvest costs. A pre-requisite to tackle this challenge was the acquisition of key information on the phenology of the coffee trees in the high-elevation equatorial climate of the Lake Toba area, and on the impact of this phenology on the bioecology of the CBB.

It is precisely because the variety *Sigarar Utang* is a local *arabica* that it was important to study its fruit set and describe how it varies according to the trees' age. In a large proportion of the plantations, the trees are left to develop freely during several years, which results in them gaining substantial height and crown volume. It was also essential to obtain data on the phenology of the cultivar Sigarar Utang, since the local climate conditions influence flowering and fruiting dynamics, and at this moment, they have never been studied. In this particular agro-climatic context, we also studied how the CBBs colonise the berries throughout the annual fruiting cycle, which is an important basis for developing an IPM program. We also studied the dynamics of infestation in relation to the age of the coffee trees, as in the case of a heavy infestation of older coffee trees, possible rejuvenation through pruning operations could bring benefits to IPM (Dufour *et al.*, 2019). Moreover, for a more theoretical purpose, we studied the distribution of CBB attacks in each tree in order to identify possible preferences. In addition, given that flight seemed to be the only means of dispersal documented so far (Roman-Ruiz *et al.*, 2018) we also examined the possibility of walking movement of CBBs between axillary nodes.

2. Material and methods

2.1. Description of the study sites

This work was carried out from March 2012 to April 2014 in the highlands of the Simalungun district, near Lake Toba (North Sumatra, Indonesia), at N 2°49' and E 98°50'. The six smallholder's plantations of *C. arabica* var. *Sigarar Utang* coffee selected for the study were located at an elevation of 1,200 m above sea level, close to three villages a few kilometres apart belonging to two different subdistricts (Pematang Sidamanik and Dolok Pardamean). The plantations were on flat ground, homogeneous and fully exposed to sunlight, and the trees were planted at 2 x 2 to 2 x 2.5 m densities. There were usually intercrops of red pepper, ginger or maize between rows. Plantation management consisted in applications of compost and chemical fertilisers three times a year for the intercrops and coffee trees. Weeding was carried out manually or chemically two or three times a year in all the plots. The trees were not pruned as in most plantations in the region, no CBB control means was used, and ripe berries were harvested at regular intervals of two to three weeks even in periods of very low production. Harvest was carried out by ourselves on the trees monitored in our study. Mean annual production of green coffee in the area reached 1,139 kg/ha (Saragih, 2012).

Temperature and humidity were measured and recorded at the study site with a Testo 175 data logger at 2-hour intervals. Rainfall data were supplied by the Tea Research and Development Center PTPN IV – Tobasari-Pematang Sidamanik. The average rainfall data from 2000 to 2011 used as a reference were provided by the same Centre (Fig 1), but no such average temperature and relative humidity were available.

2.2. Design for fruiting characteristics of *Coffea arabica* L. var. *Sigarar Utang* and observations about *Hypothenemus hampei* (Coleoptera: Curculionidae) infestation

The design consisted in six 0.5-1 ha plots of unpruned coffee trees. The first year, it comprised two 4-5-year-old plots and four 6-8-year-old plots, but the following year while the young plots were retained, the oldest were replaced by 5-year-old plots. In each of these plots, 15 coffee trees were selected according to the same sampling design, i.e. 5 coffee trees per row, 10 m apart on 3 rows spaced 20 m apart. On each tree, six productive branches were selected, either young primaries of the top of the tree or young secondaries emerging from older branches. The first year, we selected two opposite branches in the upper third of the tree, two in the middle and two in the lower third. The second year, we focused on the upper third of the trees only, selecting two branches on each of three levels within this upper third. This specific arrangement was designed to select branches bearing a greater number of nodes. Overall, according to this design, we selected a total of 6 x 15 x 6 = 540 branches, on which all our observations were carried out during the two years. The periods spanning from March 2012 to February 2013 and from April 2013 to April 2014 are referred to as Year 1 and Year 2 respectively.

During each survey repeated every 21 days, every branch was visually inspected beginning at its insertion on the trunk and working towards its tip, counting the number of infested and intact berries at each node encountered, one node having at least one berry. Thus, all deeply perforated berries within the perimeter of the apical disc were considered infested by *H. hampei* because this disc is its preferred puncture site because of its rough surface (Gumier-Costa & Faria, 2001). This species is monophagous, morphologically similar to other species of the same genus, however infested with other crops (Vega *et al*., 2015). Only *H. obscurus*, usually polyphagous could lead to confusion, but its presence on coffee is occasional (Constantino *et al*., 2011). Berries were classified into two categories: 'large unripe' (green, 5 mm or more in diameter) and 'ripe' (entirely red). Berries under 5 mm in diameter were not counted. The 5 mm size corresponds roughly to the stage at which the berries begin to become palatable to CBBs and suitable for puncturing (Salazar-Gutierrez *et al*., 1993). Mid-ripe berries were included in the 'large unripe' category. All ripe berries were harvested after each survey, throughout the two study periods.

2.3. Design for *Hypothenemus hampei* (Coleoptera: Curculionidae) short-range dispersal study

The experimental design was set up in May 2013 near the village of Manik Saribu (Simalungun district) at N 2° 49" 8"' and N 98° 50" 35"', in a single plot of 0.5 ha infested by CBBs. The objective was to assess the *H. hampei*' potential to disperse by walking along the branches. We selected six primary, productive, branches on each of ten unpruned coffee trees inside the study plot. On each of these branches, we circled the branch with glue bands (Pelton Glu®, France) between each axillary node, as well as before the first and after the last node (Fig. 2). Starting the day the bands were positioned, green, mid-ripe and ripe berries in each node were counted every two weeks over 20 weeks, distinguishing between intact and infested berries and ripe berries were harvested after each survey.The CBBs caught on the glue traps between the nodes were also counted. Females are characterised by their size, which varies from 1.5 to 1.9 mm, about 1/3 larger than the males (Roepke, 1919; Corbett, 1933; Bergamin, 1943; Vega *et al.*, 2015). According to the literature, females are always more abundant than the males but in varying proportions and the males have atrophied wings and never leave the berries (Hargreaves, 1926; Corbett, 1933; Le Pelley, 1968; Damon, 2000; Vega *et al.*, 2015; Mariño *et al.*, 2016). In this trial, the identification of some captured beetles was confirmed in the laboratory (CIRAD/France), in particular with the use of reference specimens of *H. hampei*.

2.4. Data analysis

For the multi-site study, we took into account the position of the axillary nodes on the fruiting branches (fruiting zone) by dividing each branch into three segments of subequal length: the segment closest to the trunk (branch base), the central segment, and the end segment (branch tip). Moreover, the coffee trees were divided into two age classes: 5 years and under, and 6 years and above, because differences in plant height, branch size and foliage volume could cause variations in berry production and CBB infestations.

About the phenology of *Coffea arabica* L. var. Sigarar Utang, the distribution of the counted berries per segment of the fruiting zone of each branch was analysed at the beginning of both years of study, soon after the main flowering in February. A negative binomial distribution was fitted to the data for each of the two tree-age classes using chi-squared minimisation and tested with the chi-square goodness-of-fit test.

The effect of the age of coffee trees, and the combined effect of branch level in the tree and tree age, on the production of ripe berries over the period were assessed with the data of Year 1 using two non-parametric Kruskal-Wallis rank-sum tests. Dunn's test for multiple comparisons was used to compare the levels of the variable combining the three branch levels and the two tree-age classes, with Benjamini-Hochberg's adjustment to control the experiment-wise error rate.

The fruiting dynamics was analysed in Year 1 and Year 2 on branches of the upper third only (the most productive) of the coffee trees. The variations of the total number of berries and of the proportion of infested berries were analysed in the three segments of the fruiting zone of each branch, for each tree and tree-age class. The total number of berries was assumed to vary over time, increasing after flowering and decreasing with each harvest. The proportion of infested berries was assumed to vary according to the available resource (berries) and the development conditions of the CBB population. Thus, the two were expected to have a complex non-linear relationship with time. To model this, we used a generalised additive model with mixed effects (GAMM), which incorporates nonlinear dependence. We used it with a negative binomial distribution for berries and a binomial distribution for the number of infested berries in relation to the number of intact berries. The GAMM models integrated a fixed effect of age, season and position, two smooth terms based on time, and a random effect to take into consideration the correlation between different days on the same coffee tree. The smooth terms used a thin plate spline with dependence on position for one and on age for the other to take into account the general dynamics and the differential due to position and age.

Statistical analyses were performed using R version 3.6.1 (R core Team, 2019). The fitting of negative binomial distributions was carried out using the R package vcd (Meyer *et al.*, 2020). Dunn's test for multiple comparisons was performed using the R packages FSA (Ogle *et al.*, 2020) and rcompanion (Mangiafico, 2020). The GAMM models were implemented using the R packages mgcv (Wood, 2017) and itsadug (Van Rij *et al.*, 2017). Graphs were plotted using the R package ggplot2 (Wickham, 2016).

3. Results

3.1. Climate of the Lake Toba area

The climate of the area of Lake Toba is among the most typically equatorial climates (*Encyclopædia Universalis*, 2020). According to the Köppen classification system (Peel et al., 2007), this climate corresponds to the "Cfa" class (without dry season and hot summer). The annual amplitude of temperature is very narrow and precipitations are frequent practically all year round (Fig. 3). Given that the elevation is close to 1,200 m above sea level, mean temperature is around 21°C, with a ten-day temperature amplitude rarely exceeding 10°C. Relative humidity is usually high at night but the ten-day average is approximately around 80%. Over the study period, we observed that the ten-day rainfall was quite uniformly distributed except in June and July 2012 and 2013 and in January to February 2014, when precipitations abated. Overall, these variations are in keeping with the pattern of the mean monthly precipitations recorded from 2000 to 2011 (Fig. 1). The total annual rainfall recorded in 2012 and 2013 was respectively 2,533 mm and 2,643 mm.

3.2. Phenological characteristics of *Coffea arabica*, var. *Sigarar Utang*

In the climatic conditions that prevailed locally, four flowering periods were observed annually from 2012 through to 2014 (Fig. 4). During the main major bloom, the statistical distribution of the number of berries per segment of the fruiting zone was overdispersed. Negative binomial distributions could be fitted to the data from both young 4-5-year-old coffee trees and older 6-8 year-old trees in Year 1 (X-squared = 87.0, df = 74, p-value = 0.143, and X-squared = 65.9, df = 52, p-value = 0.093, respectively), but only to the data from the older coffee trees in Year 2 (X-squared = 52.8, df = 64, p-value = 0.841). In Year 1, a large number of the axillary nodes of the fruiting zone (73% and 79% of nodes in younger and older trees respectively) failed to bear berries, but 10% of the nodes in the younger trees and 1.75% in the older trees numbered 10 berries or more. In Year 2, these age-related differences were less marked, with respectively 70% and 72% of the axillary nodes of the fruiting zone bearing no fruit, while 8% of nodes in both age groups bore 10 berries or more.

3.3. Berry production in relation to tree age and branch level

Figure 5 shows that in Year 1 the younger coffee trees were significantly more productive than the older (with a mean of 119 ripe berries on six branches *versus* 52; Kruskal-Wallis test, $p < 0.001$).

The Kruskal-Wallis test also detected a significant difference between age-classes and branch location in the tree ($p < 0.001$). Applied after the significant Kruskal-Wallis test, Dunn's multiple comparison test distinguished three classes of ripe berry production (Fig. 5). The more productive locations are the highest (67) and intermediate (50) branches of young coffee trees, followed by, in decreasing order, the higher branches of the older trees (36), the lower branches of young trees (17), and the intermediate (15) and finally lower branches of the older trees (6), these being the least productive of all.

3.4. General dynamics of *Coffee arabica* var. Sigarar Utang production and berry development in Years 1 and 2

In spite of four flowering periods every year contributing to berry production, both in Year 1 and Year 2 the total quantity of berries present on branches followed a gradually decreasing trend from March-April to February of the following year (Fig. 6). The first bloom was thus, quantitatively, the most productive. However, the four annual blooms resulted in the presence practically all year round of unripe, ripening and completely ripe berries – all palatable and attractive to CBBs.

In Year 1 and Year 2 alike, berries from flowers fertilised during the mid-February bloom (Table 1) started to reach the 'large unripe' stage in March-April (Fig. 6). Taking as reference the production of Year 2, which was greater, the mean number of berries per set of six branches increased from 117 to 126 between April and May due to the duration of the preceding flowering period. Thereafter, from May to December of the same year, the number of berries declined continuously, despite the input of young berries resulting from the second-main bloom of August and the minor blooms of May and November (Table 1, Fig. 6). These inputs can be perceived on Fig. 6, in particular on 23 August and 15 November 2013. The number of berries, large unripe and ripe taken together, reached its yearly low on 21 March 2014.

In contrast to what is seen in large unripe berries, the number of ripe berries does not increment with each passing bloom because they are regularly harvested (Fig. 6). At each harvest, their number remains fairly stable. Overall, ripe berries are present all year round but reach their annual low between February and April.

3.5. Production dynamics of *Coffee arabica* berries on high branches according to tree age and node position

Term significance in the GAMM confirmed that higher branches are more productive in young trees than in older trees (Table 2). The smooth curve of ripe berries dynamics based on predictions from the model showed that production decreased more slowly over the year in young trees than in older trees (Fig. 7A), with the latter catching up a little on this difference after some 350 days. Regarding the distribution of berries over the three segments of the fruiting zone, their number decreased from branch base to branch tip (Table 2). In the fruiting zone of upper branches, however, the dynamics observed differed depending on the segment, with an inversion of the general pattern in the course of the production period as branch tips became the more productive segment (Fig. 7B). The smooth curve of the ripe berries dynamics on the branches of all coffee trees, thus showed that production decreased regularly. In the beginning, production was significantly higher close to the trunk than in the middle of the branch, where it was greater than at the tip. The distribution of ripe berries along the branches later evened out in the middle of the period, and reversed before the end (Fig. 7B). The model explained 43% of the deviance (Table 1).

Parametric coefficients	**Estimate**	**Std. Error***	**z-value**	**p-value**
(Intercept)	3.2	0.05	70.8	< 0.001
Position: middle of the branch	-0.33	0.03	-12.4	< 0.001
Position: tip of the branch	-0.66	0.03	-23.1	< 0.001
Age: 6-8 years	-0.40	0.03	-12.5	< 0.001
Year 2	0.77	0.03	25.8	< 0.001
Smooth terms	**Edf***	**Ref.df*****	**Chi.sq**	**p-value**
s(day): age: 4-5 years	2.0	2.0	4.7	0.10
s(day): age: 6-8 years	1.6	2.1	1.5	0.51
s(day): position: base of the branch	3.7	4.0	54.1	< 0.001
s(day): position: middle of the branch	4.3	4.8	15.2	0.006
s(day): position: tip of the branch	4.1	4.6	13.1	0.03
Random effect (coffee tree)	78.8	89.0	748.3	< 0.001
Deviance explained	43%			

Table 1. Results of generalised additive mixed models (GAMM) of berries dynamics. They include the effect of position on the branch (base, middle or tip), the effect of age of the coffee trees and year of observation, two smooth terms based on the number of days (time), with dependence on age and position, and a random effect of the coffee tree.

** standard error estimates for all parameter estimates; ** edf: estimated degrees of freedom for the model terms; *** reference degrees of freedom used in statistics*

3.6. Spatial and temporal characteristics of *H. hampei* infestations

3.6.1. Infestations of the different berry stages and berry infestation dynamics according to position on branch

Over 540 branches monitored, a mean of 15.9% and 19.6% of the large unripe berries were infested in Year 1 and Year 2 respectively, and 38.8% and 53.8% of the ripe berries, with ripe berries systematically harvested every three weeks.

Term significance in the GAMM confirmed that the proportion of infested berries was generally higher on the old coffee trees monitored in Year 1 (Table 3). The smooth curve of the infestation dynamics based on predictions from the model showed that the infestation rate increased evenly until around day 340 - with a significant age-related difference that narrowed down around day 280 - then declined as the harvest was drawing to a close (Fig. 8A). The proportion of infested berries remained fairly stable whatever the position on the branch (Table 3). The smooth curve of the infested berries dynamics showed that their proportion increased gradually until around day 350 with only slight position-related differences, after which the infestations remained significantly higher closer to the trunk (Fig. 8B). The model explained 48% of the deviance (Table 2).

Parametric coefficients	**Esti-mate**	**Std. Error***	**z-value**	**p-value**
(Intercept)	-1.1	0.06	-19.7	< 0.001
Position: middle of the branch	-0.22	0.02	-12.8	< 0.001
Position: tip of the branch	-0.40	0.02	-17.8	< 0.001
Age: 6-8 years	0.65	0.03	24.9	< 0.001
Year 2	0.007	0.02	0.3	0.79
Smooth terms	**Edf***	**Ref.df*****	**Chi.sq**	**p-value**
s(day): Age: 4-5 years	2.0	2.0	48.8	< 0.001
s(day): Age: 6-8 years	3.9	4.0	125.9	< 0.001
s(day): position: base of the branch	3.7	3.9	55.5	< 0.001
s(day): position: middle of the branch	4.6	4.9	37.1	< 0.001
s(day): position: tip of the branch	4.8	5.0	131.2	< 0.001
Random effect (coffee tree)	87.3	89.0	4218.6	< 0.001
Deviance explained	48%			

Table 2. Results of generalised additive mixed models (GAMM) of fruit infestation dynamics that included the effect of tree age and year of observation, the effect of position on branch (base, middle or tip), two smooth terms based on the number of days (time), with dependence on age and position, and a coffee tree random effect.

** standard error estimates for all parameter estimates; ** edf: estimated degrees of freedom for the model terms; *** reference degrees of freedom used in statistics.*

3.6.2. Dispersal of *H. hampei* on branches

Twice monthly observations of the glue-traps on either side of the 300 axillary nodes monitored in this study showed that the first female CBBs began to appear in the traps after the first infested berries were recorded (Fig. 9). All trapped CBBs were females. Numbers of trapped CBBs never exceeded 14 individuals per observation date, and dwindled to zero as soon as no infested ripe berry remained. A total of 47 female CBBs were trapped. This number must be put into perspective because these captured females were close to nodes that have borne 335 infested ripe berries over a period of four and a half months, which implied the emergence and then flight of hundreds of other females. It should be noted that a single infested berry may harbour several dozen adults and larval stages from the oviposition (Vega *et al.*, 2015) and that more than three generations may occur (Baker, 1999).

4. Discussion

In the field, the *Sigarar Utang* variety, regarded by Hulupi & Nugroho (2013) as highly productive, was characterised by an uneven production at all levels – cluster, branch and tree. A majority of nodes bore no berry at all, while some 8% comprised more than 10. Berry production was significantly higher in young trees of 4-5 years than in older trees of 6-8 years (Fig. 5). In both cases, it was more abundant in the upper sections of the crown than in the lower parts (Fig. 5). According to Coste (1969), branches of the upper storeys are short young primary branches, more abundantly supplied in sap and therefore capable of producing more flowers and fruits. Conversely, the more meager production of the lower, older, branches can be explained by a faltering supply of sap; this situation then degrades into a completely unproductive stage, followed by a progressive drying out. A recent study in the area of Lake Toba showed that pruning these low branches produces a regenerative effect that triggers the development of secondary and tertiary shoots bearing fertile nodes, and stimulates fruiting (Dufour *et al.*, 2019). It can thus be stated that pruning the coffee trees can offset their age-related decline in productivity.

Concerning the dynamics of berry production and development, we show that the succession of blooms over the year result in the presence of berries on the branches practically at all times. This flowering and fruiting pattern, already mentioned in Dufour *et al.* (2019), is also observed in certain areas of Colombia between the 4^{th} and 5^{th} degrees of latitude North at high elevations (Arcilla-Pulgarín *et al.*, 1993). This particular phenology is related to the prevalence of a long period of frequent rains interrupted by a few short dry spells (which, in the Simalungun area, mostly take place in the beginning and middle of the year). Arcilla-Pulgarín and Jamarillo-Robledo (2003) and Ramírez-B *et al.* (2010) showed that in equatorial regions where the photoperiod is under 13 hours, the flowering of coffee trees is narrowly linked to water deficits or to high daily variations of the temperature.

In contrast to the productive pattern observed in tropical regions of Western Africa (Borbón-Martínez, 1989), Mexico and Central America (Barrera, 1994), which allows a single annual harvest only, in the Simalungun district, the staggered production combined with the frequent harvest of ripe berries results in the progressive decline of the total number of berries between April-May and February. This was observed in all coffee trees, and in particular in branches heavily loaded with fruits of the upper third of the trees (Fig. 6). It follows that berries can be found on branches over a period of at least ten months out of twelve, thus giving *H. hampei* a constant supply of food and reproduction sites next to its places of emergence.

In order to study the production pattern in greater detail, we focused on the dynamics of berry production and development in relation to the age of the trees and the position of berries on the branches. Our analyses confirm that young coffee trees were more productive than older trees (Fig. 7A) and show that at the beginning of the harvesting season berries were more numerous at the base of the branches, near the trunk, than at the tip, whereas the situation reversed towards the end of the season (Fig. 8b).

In this remarkable phenological configuration in which all the development stages of berries co-occur during most of the year, we could observe that the proportion of CBB-infested berries was more than twice as high among ripe berries (mean: 46%) as among unripe berries (mean: 18%). This trend is explained by the fact that ripe berries had been exposed to CBB attacks for longer than unripe berries, and that their potential to attract CBBs was greater (Giordanengo *et al.,* 1993; Mendoza *et al.,* 2000). This difference in attractiveness could be due to the diversity of the volatile organic compounds produced and emitted by ripe berries (Ortiz *et al.,* 2004).

Regarding the infestation dynamics, our results show that the proportion of perforated berries perceived as infested, as the number of berries was decreasing with each successive harvest (Fig. 8A and B, Fig. 7A). However, this dynamic is probably overestimated if we consider that some perforated berries, described here as infested, may have been abandoned by the colonizing females before they reach the endosperm (Ruiz-Cárdenas & Baker, 2010). We also show that aged coffee trees were always more infested than younger trees, even though this difference narrowed down during the later part of the harvest season, when the number of berries generated by the first major bloom had substantially decreased on aged trees (Fig. 8 and Fig. 7). On the other hand, the distribution of infested berries on individual branches remained fairly similar at different levels in the tree throughout the harvest season despite the variations in fruiting dynamics mentioned earlier. The co-occurrence of older, infested, berries with younger, intact, berries explains this uniform distribution of infestations. In tropical settings, where coffee trees produce a single large annual crop, colonisation tends to spread gradually, aggregatively, and to become homogeneous when infestation levels are high (Román-Ruiz *et al.*, 2018).

The dispersal of female CBBs by flight was often considered as an intangible principle, in particular in the context of the large-scale migrations that motivated the development and implementation of trapping techniques in tropical regions (Gutiérrez-Martínez *et al.*, 1995; Dufour & Frérot, 2008). However, we here demonstrate for the first time that CBBs also disperse by walking. Even though this dispersal is on a small scale, it nonetheless contributes to the progressive infestation of the axillary nodes of a branch (Fig. 9). According to our observations, dispersal by pedestrian locomotion concerns females only (as males spend their entire life cycle inside the infested berry) and occurs in the immediate vicinity of the infested ripe berry from which they emerged. This type of movement, not observed in tropical areas (Román *et al.,* 2018), reinforces the idea that, in the equatorial zone, dispersal would more often concern short distances than in tropical areas (Dufour *et al.,* 2019), at the scale of the individual branch or tree. Future experimental trapping at the scale of the plot will undoubtedly yield new elements for furthering the discussion on dispersal.

5. Conclusion

In this study undertaken in a high-elevation equatorial climate setting of the Lake Toba area in North Sumatra, we presented the phenological characteristics of the *arabica* var. *Sigarar Utang* coffee tree and their relationships with CBB infestations.

We showed: (i) how the staggered fruiting covering most of the year allowed the practically uninterrupted development of CBB infestations despite the frequently repeated harvest of ripe berries; (ii) that the older coffee trees were more affected than the younger trees; (iii) and that the horizontal distribution of infestations on individual branches remained fairly stable over time. In the ideal trophic environment that are coffee trees for CBB development, females tend to disperse by flight in search of hosts, but mainly at short range, within the tree where they emerged – which would *a priori* make this pest more difficult to control, in particular through trapping means. Trapping operations target above all females emerging from residual berries fallen on the ground, and only becomes effective in tropical areas at the time of the migration peaks that take place after the harvest, outside the fruiting period (Dufour *et al.*, 2000). The trapping trials we are considering will probably not produce the same result in number of captures, but their efficacy is still unknown. Our opinion however is that sanitation harvesting, recommended in many countries and by a number of agronomists advocating non-chemical control (Decazy, 1990; Bustillo-Pardey, 2006; Aristizábal *et al.*, 2016) could become a key tool for CBB management because it would primarily concern infested berries still on the trees, during the fruiting period. We would also recommend completing this approach with some pruning of the coffee trees, which would directly facilitate sanitation harvesting interventions (Dufour *et al.*, 2019), and with measures to prevent reinfestation by dispersing female CBBs during post-harvest operations. It will probably be necessary to identify other components of control to design a strategy for integrated CBB management in the region of Lake Toba.

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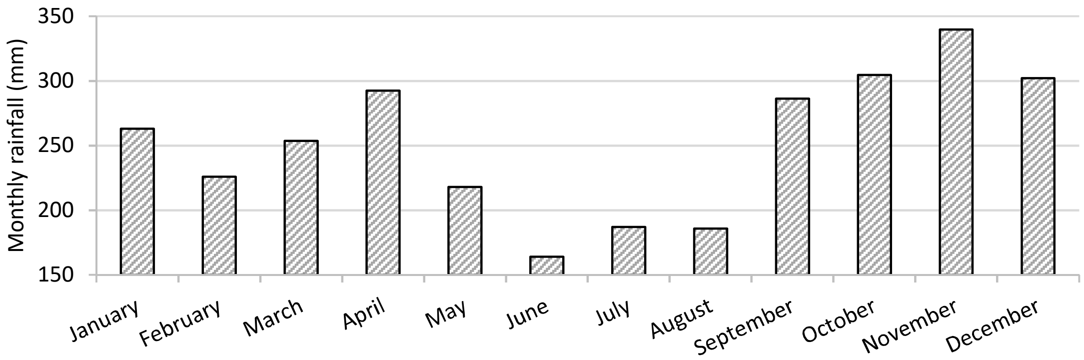

Figure 1. Average monthly rainfall in the Toba region for the period 2000-2011

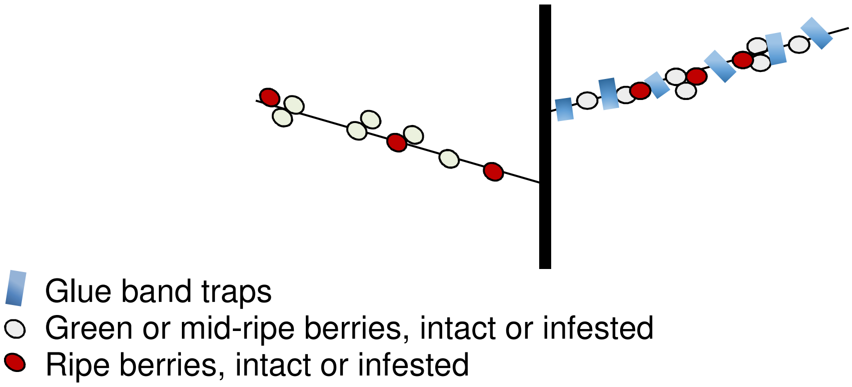

Figure 2. Experimental design for *H. hampei* short-distance dispersal. Only two branches per coffee tree are represented, with five nodes per branch

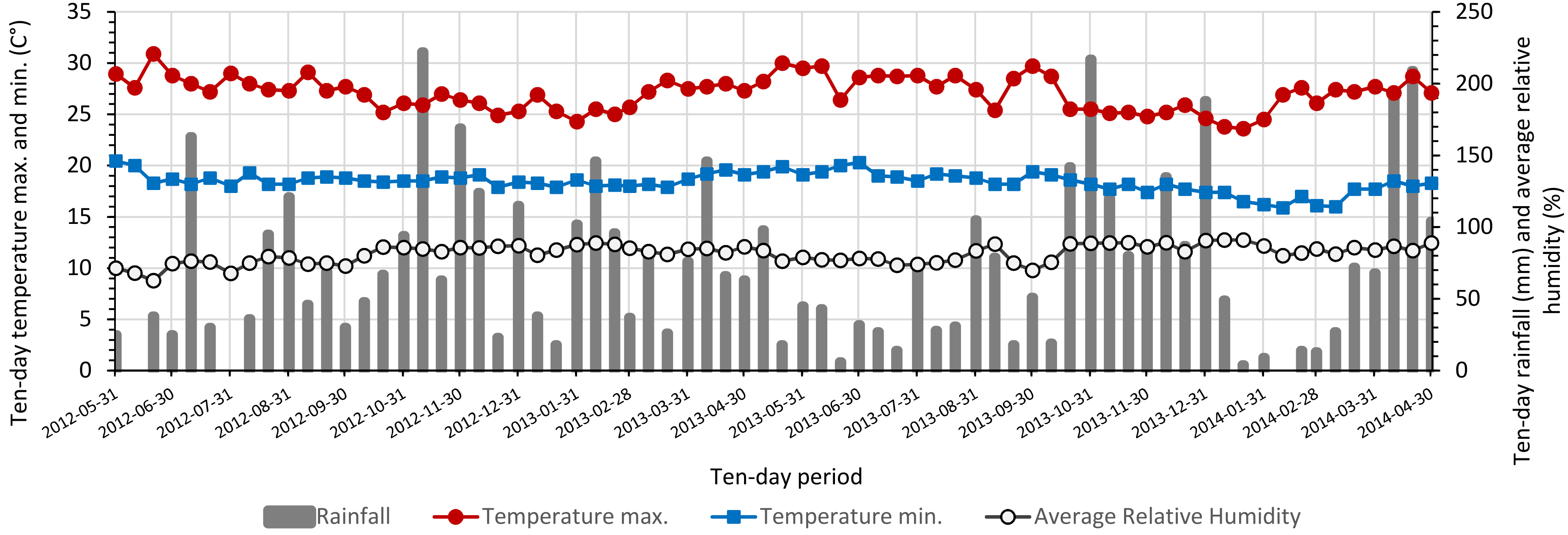

Figure 3. Climate characteristics of the Toba region from May 2012 to April 2014

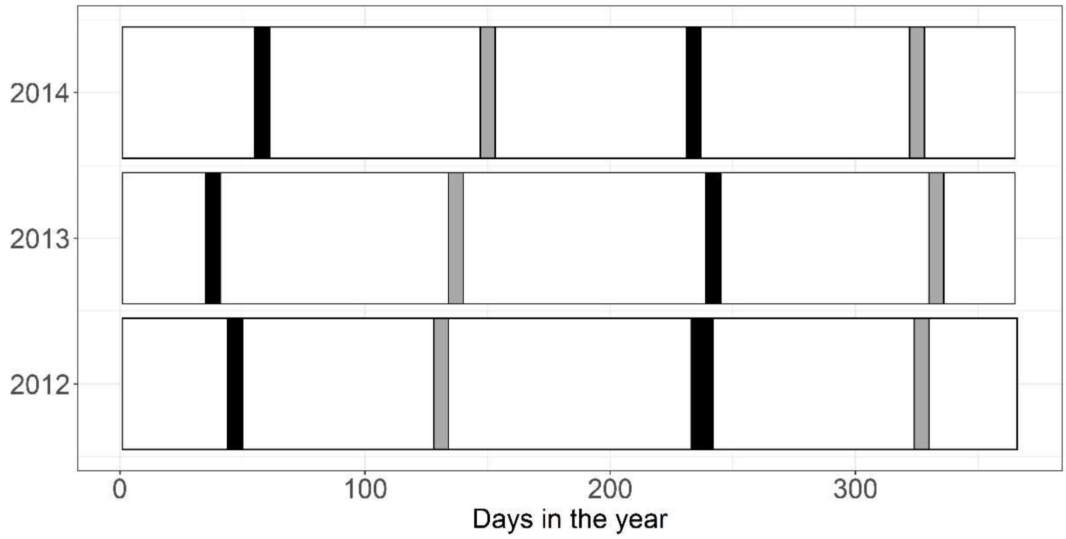

Figure 4. Annual flowering periods of coffee trees in all experimental plots. *Dark colored bars correspond to major blooms (main and second main) and light colored bars correspond to minor blooms. Small flowering bursts sometimes occur on a few trees outside the periods indicated; they are not included in the figure.*

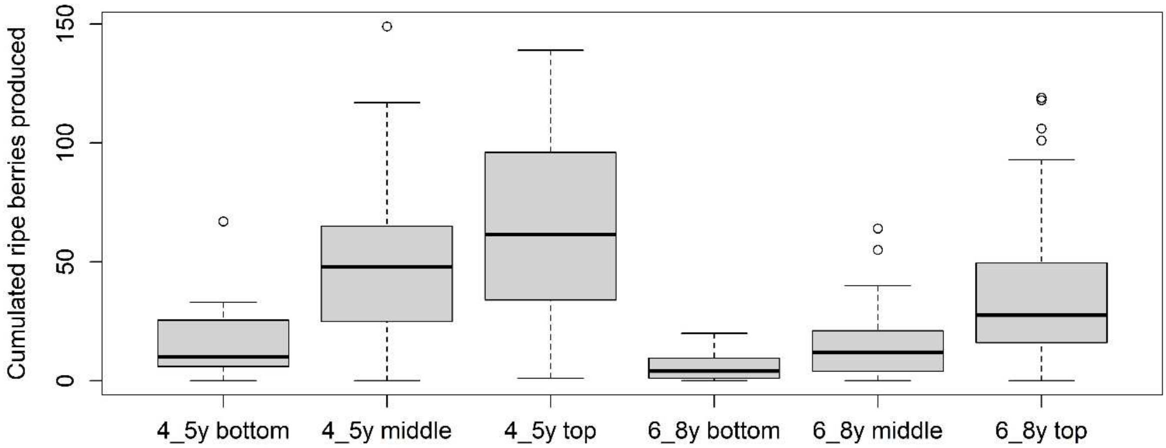

Figure 5. Cumulated ripe berry production of two branches in Year 1 according to the age of the coffee trees and the position of the branches in the tree. The thick line of the boxes-and-whisker plots represents the median. *The upper and lower edges of the boxes represent the upper and lower quartiles. The whiskers represent 1.5 times the interquartile range.*

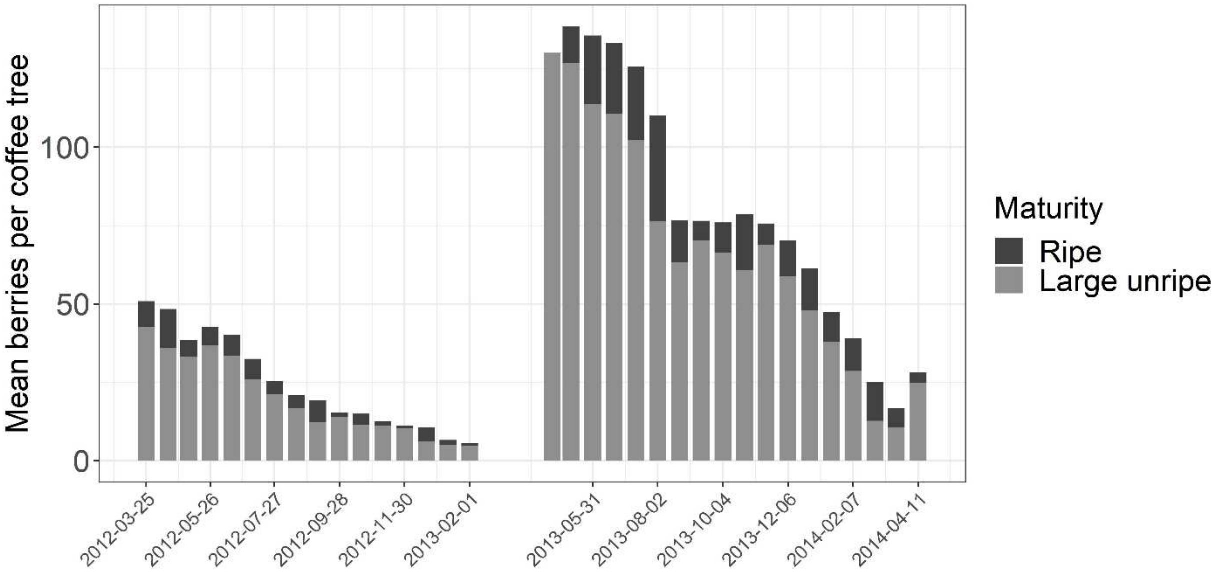

Figure 6. Production dynamics of coffee berries in Years 1 and 2 according to their stage of maturity. *Each rectangle represents the average number of berries per set of six branches at a given date.*

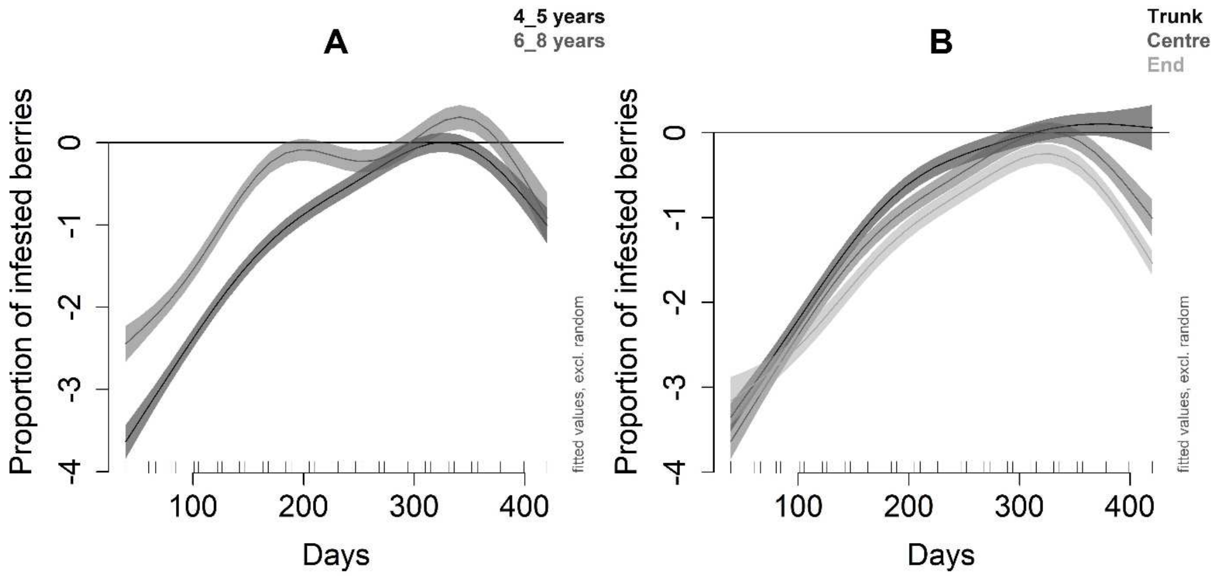

Figure 8. Variation in the proportion of infested berries on coffee trees over the period according to tree age (A) and position on branch (B). Smoothing is based on predictions from a generalised additive mixed model that included the effects of position on branch (base, middle or tip), tree age and year, two smooth terms based on the number of days (time), with dependence on position and age, and a coffee tree random effect.

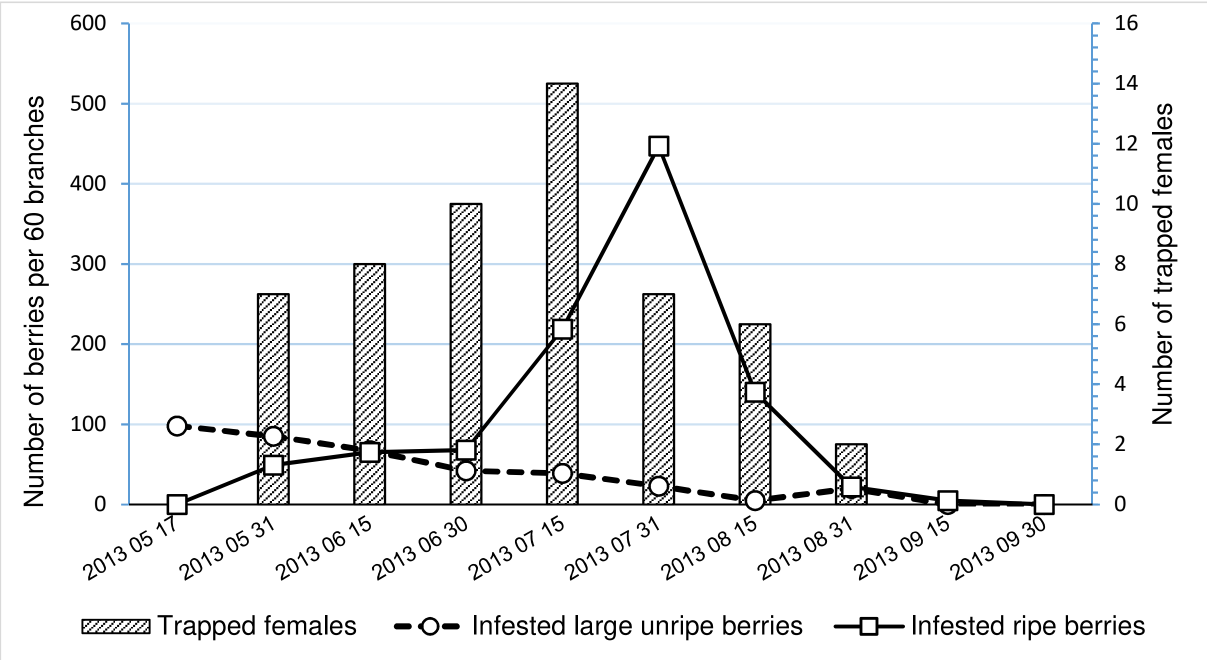

Figure 9. Number of *H. hampei* females trapped next to axillary nodes in relation to the dynamics of infestation of coffee tree branches.