LUANA DE SOUZA COVRE

Megaplatypus mutatus (CHAPUIS) (CURCULIONIDAE: PLATYPODINAE) IN A *Khaya grandifoliola* (MELIACEAE) PLANTATION IN BRAZIL

Dissertation submitted to the Plant Science Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Magister Scientiae*.

Adviser: José Cola Zanuncio

Co-adviser: Carlos Alberto Hector Flechtmann

VIÇOSA - MINAS GERAIS
2021

Ficha catalográfica elaborada pela Biblioteca Central da Universidade Federal de Viçosa - Campus Viçosa

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Covre, Luana de Souza, 1996-

C873m *Megaplatypus mutatus* (Chapuis) (Curculionidae:
2021 Platypodinae) in a *Khaya grandifoliola* (Meliaceae) plantation in Brazil / Luana de Souza Covre. – Viçosa, MG, 2021.

34 f. : il. ; 29 cm.

Orientador: José Cola Zanuncio.

Dissertação (mestrado) - Universidade Federal de Viçosa.

Referências bibliográficas: f. 26-34.

1. Besouros. 2. Armadilhas para insetos. 3. Feromônio. 4. Cairomônios. 5. Gomose. I. Universidade Federal de Viçosa. Departamento de Fitotecnia. Programa de Pós-Graduação em Fitotecnia. II. Título.

CDD 22. ed. 632.768

Bibliotecário(a) responsável: Renata de Fatima Alves CRB6/2578

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APPROVED: July 22, 2021.

Assent:

Luana de Souza Covre
Author

José Cola Zanuncio
Adviser

To the Brazilian African mahogany producers and all ambrosia beetles enthusiasts.

ACKNOWLEDGMENTS

To the Universidade Federal de Viçosa (UFV), campus of Viçosa, Minas Gerais State, and São Paulo State University "Júlio de Mesquita Filho" (UNESP), campus of Ilha Solteira, São Paulo State, for providing conditions for this research.

To the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), for granting of the scholarship for this research.

To the Postgraduate Program in Plant Sciences for their helpfulness and support during the Master's degree.

To professor José Cola Zanuncio for his guidance.

To professor Carlos Alberto Hector Flechtmann my sincere gratitude. His guidance helped me in all the time of research.

To all employees of Florestas da Canastra, in particular Adenilson Ferreira and Lancerlort Almada, for granting material and support to develop the assays.

To the laboratory assistants, undergrad and graduate students of Laboratory of Entomology at UNESP for their help with the assays carried out in the field and laboratory.

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

“Every great advance in science has issued from a new audacity of imagination.”

(John Dewey)

ABSTRACT

COVRE, Luana de Souza, M.Sc., Universidade Federal de Viçosa, July, 2021. ***Megaplatypus mutatus* (Chapuis) (Curculionidae: Platypodinae) in a *Khaya grandifoliola* (Meliaceae) plantation in Brazil.** Adviser: José Cola Zanuncio. Co-adviser: Carlos Alberto Hector Flechmann.

The ambrosia beetle *Megaplatypus mutatus* (Curculionidae: Platypodinae), native to South America, has been reported as the main insect pest in poplar plantations in Argentina and Italy. *Megaplatypus mutatus* differs from the majority of ambrosia beetle species by *M. mutatus* attacking live and vigorous host trees. In this study, we reported for the first time *M. mutatus* attacks on African mahogany trees, *Khaya grandifoliola* (Meliaceae) with a preference to trees with a DBH larger than 15 cm. Most trees had one or two attacks concentrated at heights up to 2 m high on the trunk. We discussed the plant defense mechanisms involved against *M. mutatus* attacks, and provided the first information on its flight activity in Brazil with a multivoltine flight behavior. Female beetles responded to its sex pheromone blend and pioneer males did not respond to the kairomone ethanol.

Keywords: Attack height. Gummosis. Kairomone. Pheromone. Tree trunk diameter. Voltinism.

RESUMO

COVRE, Luana de Souza, M.Sc., Universidade Federal de Viçosa, julho de 2021. ***Megaplatypus mutatus* (Chapuis) (Curculionidae: Platypodinae) em um plantio de *Khaya grandifoliola* (Meliaceae) no Brasil.** Orientador: José Cola Zanuncio. Coorientador: Carlos Alberto Hector Flechmann.

O besouro da ambrosia *Megaplatypus mutatus* (Curculionidae: Platypodinae), nativo da América do Sul, tem sido reportado como a principal praga em plantios de álamos na Argentina e Itália. *Megaplatypus mutatus* ataca árvores vivas e vigorosas, diferindo da maioria das espécies de besouros da ambrosia. Ataques de *M. mutatus* em mogno africano *Khaya grandifoliola* (Meliaceae) foram reportados pela primeira vez. Árvores com diâmetro na altura do peito (DAP) maiores que 15 cm foram atacadas por *M. mutatus.* Um ou dois orifícios, até 2 m de altura no tronco, foram encontrados na maioria das árvores atacadas. Mecanismos de defesas ao ataque e a primeira informação sobre a atividade de voo de *M. mutatus* no Brasil com comportamento multivoltino são discutidos. Fêmeas adultas, desse inseto, responderam ao conjunto de feromônios sexuais e machos pioneiros não responderam ao etanol.

Palavras-chave: Altura de ataques. Exsudação de goma. Cairomônio. Feromônio. Diâmetro. Voltinismo.

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SUMMARY

1. INTRODUCTION

African mahogany is the common name of trees of the genus *Khaya* (Meliaceae) (Lamb, 1963). Plantations in Brazil have expanded in the last decades due to the high-quality and economic value of its wood (Ribeiro et al., 2019). Thus far, most of the African mahogany timber is sold in the domestic trade market, with a yet low percentage of exported wood, mainly to the United States of America and Europe (R. Ciriello, Futuro Florestal Ltda – personal information).

Among limiting factors for this crop are damage by insects, which could threaten African mahogany wood commerce, mostly in cases where quarantine pests are associated in importing countries.

Leaf-cutting ants (*Atta* and *Acromyrmex*) and the mahogany shoot borer, *Hypsipyla grandella* (Zeller) are generally mentioned in the literature as African mahogany pest in Brazil (Falesi, 2012; Zanetti et al., 2017; Covre et al., 2018a). However, Scolytinae and Platypodinae (Curculionidae) have been reported in *Khaya* species both in nursery and field stands in several states of Brazil (Covre et al., 2018b, 2018c; Cristovam et al., 2018; Pelozato et al., 2018).

Most Scolytinae are secondary pests, attacking their plant hosts when under stressed conditions, such as injury by fire, lightning, silvicultural treatment (Wood, 1982; Flechtmann et al., 1995), and this is also the case with the majority of the Platypodinae (Milligan, 1979; Roberts, 1977a; Inoue et al., 1998; Bellahirech et al., 2019).However, there are some species known to attack primarily live trees, such as *Austroplatypus incompertus* (Schedl) (Kent & Simpson, 1992), *Dendroplatypus impar* (Schedl) (Browne, 1961), *Notoplatypus elongatus* Lea, *Platypus tuberculosus* Strohmeyer (Kent, 2001) and *Trachyostus ghanaensis* Schedl (Roberts, 1960). *Megaplatypus mutatus* (Chapuis) is included in this small list (Santoro, 1957, 1963; Alfaro et al., 2007).

Megaplatypus mutatus is native to South America, with known distribution in Argentina, Bolivia, Brazil, French Guiana, Paraguay, Peru, Uruguay and Venezuela (Reichardt, 1964). In Brazil, it has been reported in the states of Bahia, Espiríto Santo, Minas Gerais, São Paulo, Rio de Janeiro, Paraná, Santa Catarina and Rio Grande do Sul (Schedl, 1950; Reichardt, 1964; Schönherr & Pedrosa-Macedo, 1981; Zanuncio et al., 2010; EPPO, 2020).

So far, *M. mutatus* was introduced only into Italy (Tremblay et al., 2000; Griffo et al., 2012). The addition of *M. mutatus* in the EPPO/OEPP Alert list in 2004 and its inclusion as a quarantine pest in 2007 was due to the introduction into Italy and the risk it has to spread to other European countries (EPPO, 2004, 2007).

Megaplatypus mutatus is a highly polyphagous species - it may attack several live forest tree species, nuts, fruits, and ornamentals trees, mainly poplars (*Populus* spp.), and hazelnuts (*Corylus avellana* L.), in Argentina and Italy (Giménez & Etiennot, 2003; Allegro & Griffo, 2008). In Brazil, reports of *M. mutatus* host trees and attacks were restricted to native and exotic trees not in plantation conditions (Schedl, 1950; Reichardt, 1964; Schönherr & Pedrosa-Macedo, 1981; Santana & Santos, 2001; Girardi et al., 2006; Queiroz & Garcia, 2007; Carvalho Filho et al., 2008; Zorzenon et al., 2008). However, it has already been reported attacking plantations of *Populus deltoides* W. Bartram ex Marshall (CAHF, unpublished data), *Eucalyptus* spp. (Pinheiro, 1962), *Eucalyptus saligna* Smith (Flechtmann et al., 2004) and two hybrid species of *Eucalyptus* plantations (Zanuncio et al., 2010).

Megaplatypus mutatus shows a preference to attack live and healthy trees, which have a diameter at breast height (DBH) of 15 cm and higher (Santoro, 1957; Casaubon et al., 2006; Lucia et al., 2014). Direct damage is generated by galleries they tunnel into trunks of live and healthy trees, which then turn more prone to be broken by the wind (Santoro, 1957). Indirect damage results from the staining of the wood, due to the action of their symbiotic blue-staining fungi which grow out of their galleries (Santoro, 1957; Guerrero, 1966).

This beetle has a cryptic behavior, where it spends the vast majority of its life cycle hidden and protected in galleries inside host trees (Santoro, 1957). For this reason, the efficiency of the use of insecticides for its control is low (Griffo et al., 2012). It appears the best tool to help controlling *M. mutatus* is the use of its pheromone bouquet as a mating-disruption technique (Funes et al., 2011; Gonzalez-Audino et al., 2013; Funes et al., 2016; Ceriani-Nakamurakare et al., 2017). Pheromones may also be used to monitor for this borer (Funes et al., 2009; Gonzalez-Audino et al., 2011).

We recorded for the first time in the state of Minas Gerais, Brazil, attacks of *M. mutatus* on trees of *Khaya grandifoliola* C. DC.. Our goals were (1) to monitor and assess the efficiency of a group of semiochemicals in flight intercept traps in Brazil, (2) to study the flight activity and seasonality of *M. mutatus*, and (3) to evaluate the damage potential of this beetle species in *K. grandifoliola* trees in a plantation in Minas Gerais.

2. MATERIAL AND METHODS

2.1. Study Sites

Study sites were stands of different ages of African mahogany, *K. grandifoliola* (20°7'30.73"S 46°27'32.56"W), in Fazenda Taquaril, in São Roque de Minas, state of Minas Gerais, Brazil (Table 1).

Table 1. Stand number, planting date (month/year), stand age (months), diameter at breast height (DBH) (centimeters) based on inventory, area (hectares) and number of ethanol (EtOh) and pheromones (phero) (sulcatol, sulcatone and 3-pentanol) baited flight intercept traps deployed in each African mahogany (*Khaya grandifoliola*) stand in São Roque de Minas, Minas Gerais, Brazil

stand # (planting date)	age[1] (months)	DBH (cm) 2016	2017	2018	2019	2021	area (ha)	# traps EtOh	phero
1 (Mar2010)	75	20.6	23.1	25.0	26.6	33.0	56.2	4	11
3 (Dec/2012)	40–42	12.2	15.1	18.8	21.6	29.4	52.3	10	0
4 (Feb/2013)						31.0	22.5	2	0
5 (Jan/2013)						31.8	44.7	5	0
6 (Jan/2013)						30.5	8.1	3	0
7 (Feb/2013)						27.0	8.6	2	0
8 (Feb/2013)						28.8	19.5	5	0
9 (Dec/2013)	30	7.5	11.5	15.6	19.5	29.9	6.0	1	0
10 (Dec/2013)						29.4	29.2	3	0

[1] age at the time of the beginning of the experiment, June 2016

2.2. Inspection of Trees Attacked by *Megaplatypus mutatus*

Trees with symptoms of attack by *M. mutatus* were inspected infrequently from July 2016 until April 2021. The number of active holes (where sawdust was expelled), inactive holes (holes clogged with gum exuded by trees), and respective height above the ground were measured. We divided the height above ground of the holes into five 50 cm-intervals, (1) from ground level up to 50 cm, (2) from 51 cm to 100 cm, (3) from 101 cm to 150 cm, (4) from 151 to 200 cm, and (5) above 200 cm. Whenever DBH of attacked trees was not measured individually, we used inventory values for the whole stand.

2.3. Seasonality and Semiochemical Assays

Flight intercept traps (modified from Berti Filho & Flechtmann, 1986) were baited either with 96% ethanol or a blend of the *M. mutatus* pheromonal components sulcatol, sulcatone and 3-pentanol (Gonzalez-Audino et al., 2005; Gatti-Liguori et al., 2008a), each in individual sachets, but added together in each trap (Table 1). The release rate of the pheromones was 10.0, 7.8 and 40.0 mg/d at 25°C (ChemTica International, S.A., Costa Rica), respectively, while that of ethanol was 870 mg/d at 20°C. The pheromones were changed every three months and ethanol was replaced every week. The trapping frequency was weekly from August 05, 2017, until September 28, 2018, equaling 60 trapping weeks.

Voucher specimens of trapped beetles are deposited in the Museu de Entomologia da FEIS/UNESP (MEFEIS), Ilha Solteira, state of São Paulo, Brazil.

Daily air temperature (maximum, minimum and mean), mean air relative humidity and rainfall were obtained from the Meteorological Station “A565” (20°1'52.00"S 46°0'31.00"W) of The Instituto Nacional de Meteorologia (INMET) in Bambuí, Minas Gerais, and distant less than 48 km from the sampling site.

We divided the collecting period into a “rainy season”, with higher temperatures and more rainfall, and the remaining period into a “dry season”, with colder temperatures and less rainfall (Flechtmann et al., 1995; Covre et al., 2021). We predetermined here that “dry season” would be the period between 5 August until 22 September 2017 and 13 April until 28 September 2018, while “rainy season” would fall between 23 September 2017 until 12 April 2018; we used statistical analyses to corroborate this division.

Meteorological data averages and *M. mutatus* trappings between “seasons”, and beetle catches between lures (ethanol vs. pheromone) were compared using the generalized linear model (Proc GLM) and treatment means were separated by the Tukey test at 5% of significance. Hole height intervals were compared by Kruskal-Wallis test (proc NPAR1WAY Wilcoxon) SAS Institute 1990).

3. RESULTS

3.1. Inspection of Trees Attacked by *Megaplatypus mutatus*

We visited the site in June 2016, when for the first time damage by *M. mutatus* on trees was observed by employees. Damage was limited to stand 1, the oldest stand in the plantation, and with the highest DBH (Table 1). At this time, we cut down a tree with three active *M. mutatus* holes. Holes at 0.8 m and 1.61 m above ground were colonized by a couple each, while the third hole, at 1.5 m height, had only a male pioneer beetle in it. In all cases, beetles were alive and at the end of short galleries, a hint that the attacks were recent.

Inspections in the plantation started in July 2016. A total of 37 trees were then being attacked, corresponding to less than 1% of all trees. Average number of holes/tree was 1.5 (1 – 5). In all, 54 holes were counted, where 83% of them were active (releasing frass), while 17% were inactive (gum secreted by trees apparently successfully killed the invading beetles). Beetles bored into the trunks from a height of 5 cm above-ground up to 3 m from the soil; however, 75% of holes were between 0.5 cm to 1.5 m height. The attacks followed a clumped distribution, being concentrated to an area of 13 ha in the northern part of the stand (20°06'23.76"S 46°27'29.88"W).

In January 2018 we surveyed the whole stand 10 (20°07'30.8"S 46°26'05.1"W), whose tree DBH average was 15.6 cm (Table 1). For the first time we recorded a single attacked tree there. There was only one hole in the attacked tree, at 20 cm height, and filled with gum – hence inactive. This tree was cut down, and one dead male *M. mutatus* was found right underneath the bark, indicating the tree was able to resist the attack.

In July 2018 we surveyed less than 50% of stand 5 (20°07'13.65"S 46°26'53.96"W) and stand 8 entirely (20°07'26.11"S 46°27'48.72"W). In stand 5 three trees were attacked, one with an active hole, another one with an inactive hole, and a third tree with two inactive holes. All holes were within 1 m height in the tree trunks. No attacked trees were found in stand 8.

In December 2019 we surveyed the southern part of stand 1 (20°06'28.14"S 46°27'35.46"W) which was mostly not surveyed in July 2016. Two ‘new’ attacked trees were found, one of them with one inactive hole, and another with one active hole. One tree in this southern part which in our July 2016 survey had two holes, was cut down. No hole was found, indicating the tree was able to overcome the attack and seal the holes to a point no scar was to be found as the remainder of the beetle external boring activity.

Stand 1 was again surveyed, nearly in its entirety, in March 2021, because it was the most attacked stand in all previous surveys. We also surveyed less than 50% of each stands 5 and 7 (20°07'38.07"S 46°27'33.51"W). In stand 1, only two attacked trees were found, in its southern portion, one tree with an inactive hole (DBH = 32.5 cm; hole height = 126 cm), and another with one active hole (DBH = 45.0 cm; height = 37 cm). No attacked trees were found in stands 5 and 7.

In April 2021 we surveyed less than 50% each of stands 3 (20°07'7.84"S 46°27'29.45"W), 6 (20°07'46.94"S 46°27'7.59"W), 7 and 10. In all of them *M. mutatus* attacks were observed. In stand 3 there were three attacked trees (average tree DBH = 28.9 cm), each with one inactive hole. In stand 6 we found two trees (average tree DBH = 30.6 cm), one with an inactive hole, and another one with two inactive holes. Two trees with one inactive hole each were found in stand 7 (average tree DBH = 29.3 cm). In stand 10 there were 8 trees (average tree DBH = 28.3 cm) with *M. mutatus* holes; six trees with one inactive hole each, one tree with six inactive holes, and one tree with an active hole, this one apparently recently initiated.

Not all *M. mutatus*-attacked trees had their DBH measured in our surveys. If we use the inventory stand DBH (Table 1) for those cases, the DBH average of attacked trees was 23.3 cm (15.6 cm – 45.0 cm; n = 62 trees). However, if taken into account only trees whose DBH was actually measured, the average increased to 27.84 (21 - 45; n = 18 trees).

The observed number of holes per tree varied from one to six, but the vast majority of attacked trees had only one hole (Figure 1).

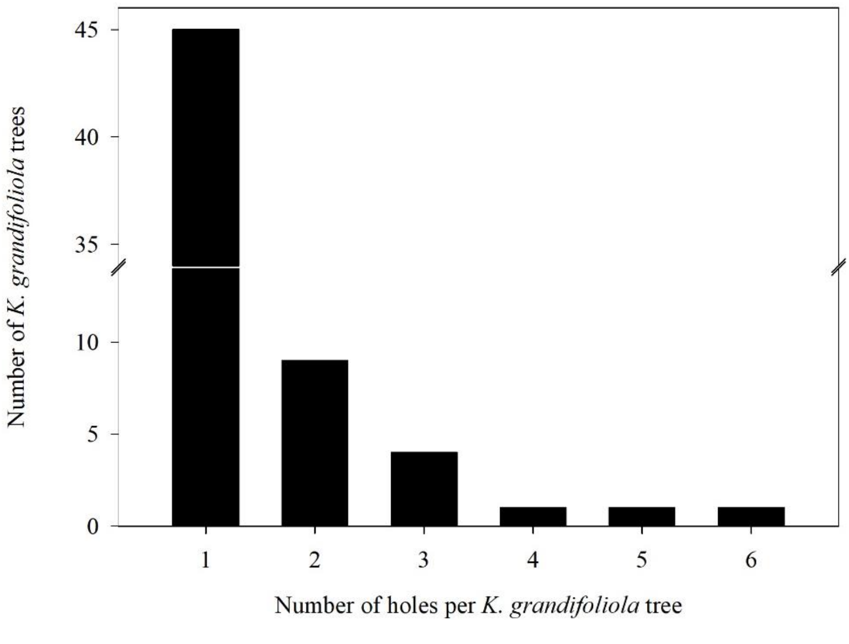

Figure 1. Number of holes of *Megaplatypus mutatus* per *Khaya grandifoliola* tree in São Roque de Minas, Minas Gerais state, Brazil from June 2016 to April 2021.

Attacks could be found from 2 cm above ground until 3 m in the trunk. However, attacks were concentrated in heights lower than 2 m, with a slight preference for the range between ground level up to 0.5 m above the soil (Figure 2). There were statistically significant differences among treatments (χ^2 = 81.77, P < 0.0001). Overall, we observed 82% mortality (n = 90 holes) in nest initiation in *M. mutatus*.

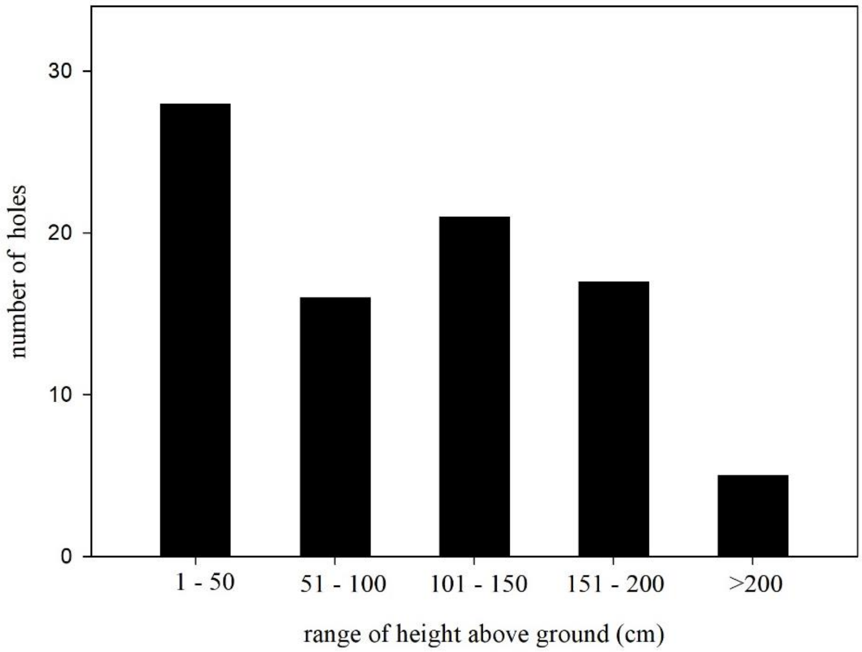

Figure 2. Range of height of *Megaplatypus mutatus* holes above ground in *Khaya grandifoliola* trees in São Roque de Minas, Minas Gerais state, Brazil from June 2016 to April 2021

3.2. Seasonality and Semiochemical Assay

Values for rainfall ($F_{1,59}$ = 23.46, *P* < 0.0001), air relative humidity ($F_{1,59}$ = 7.50, *P* = 0.0081) and maximum ($F_{1,59}$ = 18.87, *P* < 0.0001), minimum ($F_{1,59}$= 111.31, *P* < 0.0001) and mean temperatures ($F_{1,59}$ = 123.29, *P* < 0.0001) were significantly higher during the "rainy season" when compared to the "dry season". These results validated our division of the trapping period into "rainy" and "dry" seasons (see Figure 3).

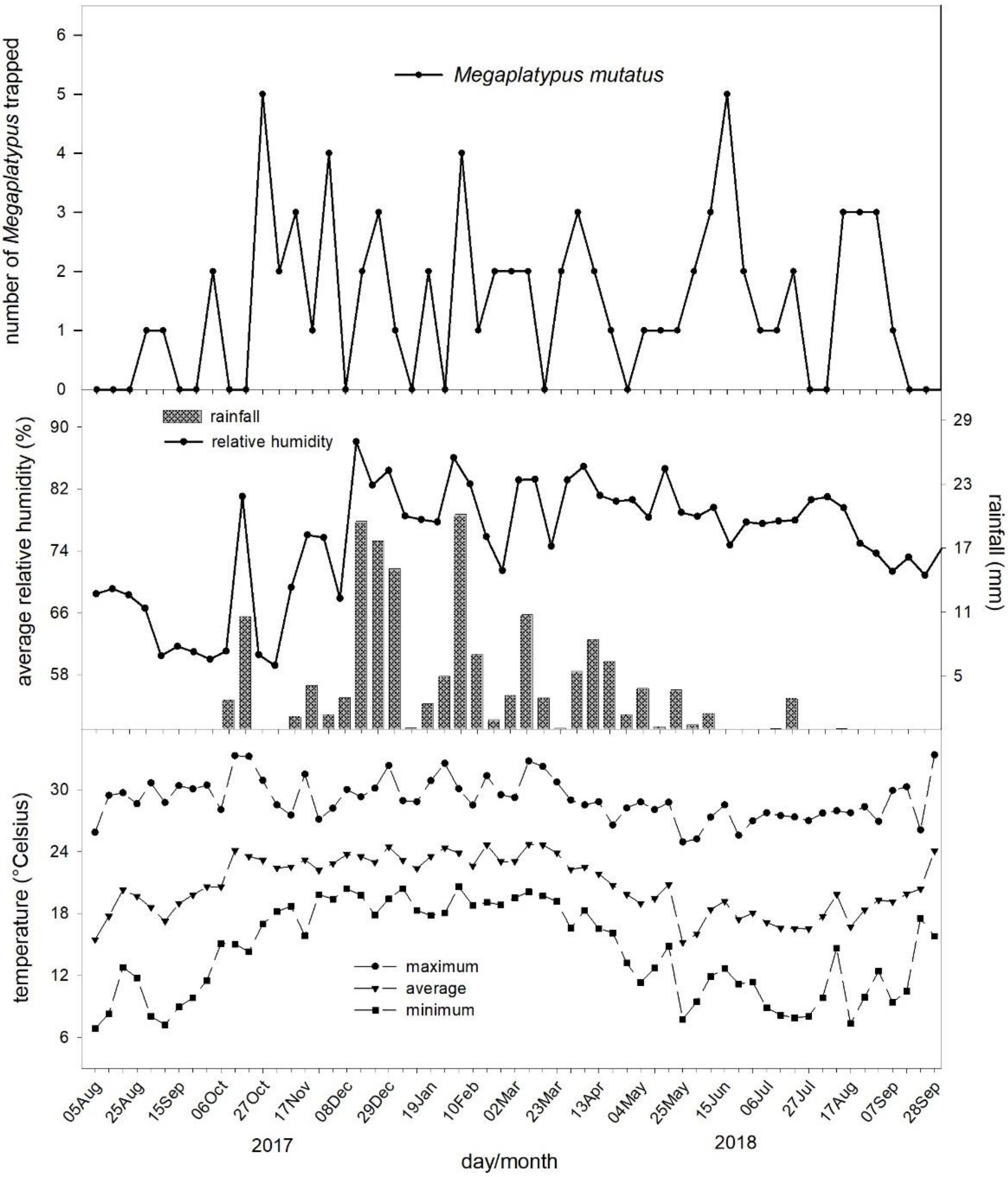

Figure 3. Total of *Megaplatypus mutatus* trapped in pheromone-baited flight intercept traps in African mahogany, *Khaya grandifoliola* stands in São Roque de Minas, Minas Gerais state, Brazil and weekly values of mean rainfall, relative humidity, and temperature (maximum, average, minimum).

We trapped a total of 8 male and 73 female *M. mutatus* specimens, all of them in pheromone-baited traps, which hence proved more attractive to this species than 96% ethanol ($F_{1,59}$ = 27.18, P < 0.0001). There was no statistically significant difference in *M. mutatus* catches between seasons ($F_{1,887}$ = 2.55, P = 0.1109).

4. DISCUSSION

Megaplatypus mutatus has already been reported attacking several Meliaceae species, including *Melia azedarach* L., *Cedrela fissilis* Vell. and *Cedrela* spp. (Schedl, 1950; Santoro, 1960; Giménez & Etiennot, 2003). This is the first time *M. mutatus* is reported attacking a *Khaya* species, *K. grandifoliola* to be specific, and in a commercial plantation.

We surveyed for *M. mutatus* attack six times, equally distributed in both 'dry' and 'rainy' seasons. In the vast majority of the cases, *M. mutatus* attacked apparently healthy trees. Among the few Platypodinae known to attack live and apparently healthy trees, there is a group of species (*A. incompertus*, *D. impar* and *P. tuberculosus*), hereafter classified as 'A1', which attack and develop exclusively in hosts under such conditions (Browne, 1961; Kent & Simpson, 1992; Kent, 2001). In another group, hereafter classified as 'A2' (*N. elogatus* and *T. ghanaensis*), they will attack live trees that are also under some sort of stress (Roberts, 1960; Kent, 2001). While based on the literature *M. mutatus* would be classified as 'A1', in a few occasions we found males initiating their attacks from scars originated from forestry implements or underneath trunk canker growths. If these observations are taken into consideration, *M. mutatus* should better be classified as an 'A2' species.

In addition to attack live trees, *M. mutatus* has a strong preference for trees with a DBH 15 cm and higher (Santoro, 1957; Casaubon et al., 2006; Girardi et al., 2006; Marquina et al., 2006; Lucia et al., 2014). Roughly, trees reached a minimum of 15 cm DBH when they were five years old, under local site conditions. In our experiment, the DBH average of attacked trees was above 23 cm, matching with reports from the literature. In all species known to have live trees as hosts, group 'A' ('A1' plus 'A2'), they attack only trees with a high DBH, higher than 19 cm (Roberts, 1960; Browne, 1961; Kent, 2001). For the vast majority of species which will attack stressed, dying or felled trees – hereafter classified as 'B' species, apparently there is no preference for a particular minimum DBH, which could vary, often within a species, from twigs a few centimeters wide to trunks as large as 15–20 cm in DBH. Some examples of 'B' species are *Crossotarsus externedentatus* (Fairmaire), *Dinoplatyus calamus* (Blandford), *Euplatypus parallelus* (Fabricius), *Platypus apicalis* White, *Platypus gracilis* Broun, *Platypus subgranosus* Schedl and *Treptoplatypus caviceps* (Broun), to name a few (Milligan, 1979; Roberts, 1977a; Elliott et al., 1987; Hijii et al., 1991; Li et al., 2018). Three notorious exceptions to this list of 'B' species are *Platypus cylindrus* (Fabricius) (DBH > 20 cm; Bellahirech et al., 2019) *Platypus gerstaeckeri* Chapuis (DBH > 14 cm;

Roberts, 1977a) and *Platypus quercivorus* (Murayama) (DBH > 14 cm; Hijii et al., 1991) where minimum DBH reported in the literature of attacked hosts is above 14 cm.

It is not yet established why ‘A’ species attack only trees with a high DBH. This might be due to two factors, which might act combined or individually, the species gallery pattern and its body size. For some of these species the gallery pattern requires quite some space to be built. This seems to be the case at least with *D. impar* and *M. mutatus*, where the gallery is built in a transverse plane, and curves gradually in a spiral close to the center of the heartwood (Santoro, 1957; Browne, 1961). This should also be the case with *A. incompertus*, a social species, in which the gallery system grows over the years, and where there is a relationship between tree size and the volume of wood available to support the colonies (Kent & Simpson, 1992; Kent, 2001; Smith et al., 2018). Along this rationale, it is implied that *M. mutatus* has a preference for higher DBH host trees for they provide more room for offspring development (Marquina et al., 2006), which can be as high as ca. 200 emerging adults on average from one single parental gallery (Santoro, 1963). In addition to the gallery factor, for some Scolytinae species its body size is directly correlated with host diameter preference (Beaver, 1977). All ‘A’ species could be classified as larger species, species with body length 5 mm and larger (Chapuis, 1865; Lea, 1910; Strohmeyer, 1910; Schedl, 1936, 1959,1968), when compared to ‘B’ species (Milligan, 1979; Candy, 1990; Hijii et al., 1991).

Over 73% of the attacked trees had only one hole *M. mutatus* pinhole, and trees with up to two holes comprised ca. 89% of our sample size (Figure 1). While for ‘B’ species the number of holes found per tree is usually high (Roberts, 1968; Milligan, 1979; Lee et al., 2011; Bellahirech et al., 2019), for ‘A’ species it is low (Browne, 1961; Santoro, 1963; Roberts, 1968). It is worthwhile pointing out that when pheromones are involved in ‘A’ species, which was so far reported for *A. incompertus*, *M. mutatus* and *T. ghanensis*, it is a sex pheromone – aggregation pheromones were not yet reported in this group (Roberts, 1968; Kent, 2001; Gonzalez-Audino et al., 2005). However, in ‘B’ species, aggregation pheromones seem to be common, having been already reported for *P. apicalis*, *P. cylindrus*, *Myoplatpypus flavicornis* (Fabricius), *P. gracilis*, *P. koryoensis* and *P. quercivorus*, to name some (Madrid et al., 1972; Milligan, 1982, Milligan et al., 1988; Algavario et al., 2002; Tokoro et al., 2007; Kim et al., 2009). Sex pheromones usually attract mainly the opposite sex of the beetle which is releasing it, while aggregation pheromones attract conspecifics from both sexes, and in larger numbers (Symonds & Gitau-Clarke, 2016 and references therein). Perhaps this apparent lack of aggregation pheromones is the reason why ‘A’ species attack trees in low numbers, while ‘B’ species might be found in much higher numbers when they colonize their hosts.

Attacks on tree trunks were observed for heights up to 3 m above ground. These results are similar to those found in cases where *M. mutatus* was reported attacking a number of Brazilian native trees (Girardi et al., 2006; Queiroz & Garcia, 2007) and *Eucalyptus* clones (Zanuncio et al., 2010) in Brazil, and *Populus deltoides* in Argentina (Landi et al., 2011) and Brazil (CAHF, unpublished data). However, *M. mutatus* is able to attack much higher up in the trunks, as reported in Argentina (Santoro, 1960; Marquina et al., 2006). Here we report for the first time the height preference of attack in tree trunks. Most attacks were concentrated from ground level up to 2 m high, with a slight preference for the range up to 50 cm of height; there was a sharp drop in observed attacks at heights higher than 2 m (Figure 2). Those results are similar to what was observed in *P. koryoensis* (Lee et al., 2011) and in *P. quercivorus* (Igeta et al., 2004). Perhaps attacks were concentrated at lower trunk heights because tree diameter increases the closer it gets to the tree base.

One strategy to overcome tree resistance by colonizing beetles is by mass-attack, a well-known phenomenon in Scolytinae bark beetles (Six, 2020 and references therein). It seems though that for 'A' species of Platypodinae, there is not such a behavior (Browne, 1961; Roberts, 1968; Kent, 2001), and trees are usually attacked by a low number of individuals, as previously discussed. In our study, *M. mutatus* fit the general pattern reported in the literature for 'A' species (Santoro, 1957; Santoro, 1963; Girardi et al., 2006) - in the majority of attacked trees, there were only single or double attacks (Figure 1). Number of attacks of three and greater were exceedingly rare, and the maximum number was six (Figure 1). However, for 'B' species (see list of species provided above), reports of mass-attacks on host trees seem to be the rule (Roberts, 1976; Milligan, 1979; Hijii et al., 1991; Lee et al., 2011; Bellahirech et al., 2019).

There is not much information in the literature regarding the distribution of Platypodinae species within a forest or plantation. *Platypus apicalis*, *P. gracilis* (Milligan, 1979) and *P. quercivorus* (Yamasaki et al., 2014), all 'B' species, are reported to have a clumped distribution. *Platypus subgranosus*, another 'B' species, shows also a clumped distribution, but apparently this species is just following the distribution of its diseased host trees, which typically have a clumped distribution (Elliott et al., 1987; Candy, 1990). While in our study the distribution of attacked trees was to be clumped, it seems that under certain undefined conditions it might also be at random, as observed in Argentina (Gonzalez-Audino et al., 2005).

When attempting to colonize trees, there is always a certain percentage of failure involved in establishing nests in platypodines (and surely for other beetle borers, for that matter). Roberts (1968) listed the most important failure components in platypodines as mating failure, host resistance, failure in growing the symbiotic ambrosia fungi, and natural enemies. We found a very high percentage of aborted male-attacks – the pioneer sex (Santoro, 1957) in our experiment. Under present conditions, we consider we can rule out three of the four factors listed above as the major *M. mutatus* beetle mortality.

The number of pioneer male beetles is low, and the sex ratio in this species is 1:1 (Santoro, 1963). Hence, chances of pheromone-calling males to attract a mate could be considered fair, discarding the importance of this factor. A number of fungi associated with *M. mutatus* were already reported (Guerrero, 1966; Ceriani-Nakamurakare et al., 2016, 2018, 2020), but it is unlikely this was a reason for the high observed mortality in our experiment due to the fact beetles died in the very early stages of tree colonization, without a chance to even start growing their symbiotic fungi, rejecting this possibility. All beetles we found in dissections were intact, dismissing this option as well.

Platypodines in many occasions fail to establish nests, because they are not able to overcome the attacked plant defenses. One mechanism of tree defense involves the presence of gum. The existence of gum is spread among families of several tree species, including Meliaceae (Pennington & Styles, 1975). In *Khaya* species (Meliaceae) gum is found in phloem vessels (Panshin, 1933), pores (Donkor 1977) and in the secondary xylem (Pennington & Styles 1975). There are several factors that cause the exudation of gum, gummosis, and among those are injuries inflicted by insects (Jones, 1959; Taylor, 1960; Irvine, 1961; Roberts, 1969; Roberts, 1977b; Nussinovitch, 2010). This gum exudation acts as a physical defense against invading insects, encircling and embalming them when they bore through the bark (Jones, 1959). The chemical constituents of *Khaya* species's gum contain several secondary metabolites (Konno, 2011), and have been extensively studied, including those of *K. grandifoliola* (Aspinall et al., 1956; Aspinall & Bhattacharjee, 1970; Banerji & Nigam, 1984; Guimarães, 2007). These secondary metabolites may constitute a secondary line of defense, chemical one, against insect borers (El-Aswad et al., 2004; Konno, 2011).

Gummosis as a defense mechanism against platypodines is well known, having already been reported in *A. incompertus*,*C. externedentatus* (Roberts, 1977a), *P. apicalis*, *T. caviceps*, *P. gracilis*, *Trachyostus aterrimus* (Schaufuss), *Trachyostus carinatus* Schedl, *T. ghanaensis* and *Trachyostus schaufussi schaufussi* Strohmeyer (Roberts, 1968; Wright & Harris, 1974; Milligan, 1979), whether these beetle species are attacking native or exotic tree species.

In the majority of the cases when *M. mutatus* beetles were observed attacking trees, we found dead males that were either pitched out or encircled by gum exudation at the entrance of their bored holes. In only one occasion we found two couples - alive - inside short galleries, indicating a recent attack. However, in another occasion, a tree that had two holes in July 2016, which was then cut in December 2019, had no evidence of the attack anymore. This might suggest that secondary plant defenses might have acted, killing the attacking beetles, and that there had been no time yet for these defenses to have played their role in the case where we found the two live couples. The resistance of the tree against *M. mutatus* beetles seems to have two layers. There is an initial line of defense, when the attacking beetle bores into the phloem, causing the tree to exude gum, which either expels or engulfs it, which accounted for the vast majority of the cases here. In the case where the beetles managed to escape the initial gum defenses, the action of likely toxic secondary compounds played then a role, killing the beetles who managed to reach the softwood of the trunk.

Gummosis has been reported for *M. mutatus* in *Acacia dealbata* Link*, Acacia mearnsii* De Wild, *Ailanthus altissima* (Mill.), *Eucalyptus viminalis* Labill., *Eucalyptus* clones, *Melia azedarach* L. and *Pinus taeda* L., where the gum (or resin, in the case with *P. taeda*) acted as a mechanic defense mechanism against the beetle (Santoro, 1957, 1960; Zanuncio et al., 2010). It is reported here for the first time in *K. grandifoliola*.

In our experiment, with the use of pheromone-baited traps, the flight period was observed throughout the year (Figure 3), and there were no differences in catches of *M. mutatus* in pheromone-baited traps between seasons. This implies that monitoring for this species should be done throughout the year, when necessary. The only similar experiment done in Brazil focused only on the activity of beetles while developing inside live *Paubrasilia echinata* (Lam.) trees, which seems to take place throughout the year, but unfortunately no seasonality data were provided (Girardi et al., 2006).

Our results contrast with the behavior of the beetle in northeastern (provinces of Entre Rios and Buenos Aires) and southern Argentina (province of Rio Negro), where there is a more distinct flight activity pattern. In northeastern Argentina the flight period coincides with the warmer and rainier months from September through February (spring through summer seasons), with a higher activity concentrated between November and December (Santoro, 1957, 1963; Funes et al., 2011, 2016). Beetles might also continue to fly during the fall and winter, when temperatures are higher than normal (Toscani, 1990). In southern Argentina the flight period lasts a little longer, encompassing the months of November through May (spring through fall) (Thomas, 2011). In Italy, where *M. mutatus* was introduced (Tremblay et al., 2000; Griffo et al., 2012), *M. mutatus*'s flight activity in the southwest (region of Campania) lasts from May to September (spring through summer) (Funes et al., 2011; Gonzalez-Audino et al., 2013; Funes et al., 2013).

There is a difference in voltinism in *M. mutatus* according to the region of study. In our site it a clearly showed multivoltine behavior (Figure 3), while in Argentina it is basically univoltine (Santoro, 1957, 1963; Toscani, 1990; Thomas, 2011). However, under certain conditions, it appears might be bivoltine as well (Gatti-Liguori et al., 2008b; Gonzalez-Audino et al., 2011). In Italy, despite some overlapping in a few collecting sites, it seems the species is might be bivoltine (Funes et al., 2011; Gonzalez-Audino et al., 2013). In NE Argentina the average winter temperature ranges between 11-12°C (Casaubon et al., 2006) and in SW Italian sites, 9-11°C (Fato et al., 2004), some 6-7 degrees lower than in our site, where site average winter temperature was ca. 18°C. Temperature is a key regulator of the annual cycle of insects, and this reflects in the voltinism of the species (Annila, 1969). Overall, in colder climates there is a trend for a species to be univoltine, and in warmer climates, to be multivoltine (Schebeck et al., 2017 and references therein). In this sense, we would expect that, if seasonality were to be studied in Brazil in a region colder than where this study was done (further south), we would see *M. mutatus* shift from a multivoltine to a univoltine life cycle, resembling the predominant behavior seen in Argentina and in some Italian sites, as mentioned above.

No specimens whatsoever of *M. mutatus* were trapped in our ethanol traps. We would expect that if beetles were trapped, they would have been males, the pioneer sex (Santoro, 1963), which would likely be attracted to host kairomones (Lucia et al., 2014). However, our results were somewhat expected. Ethanol is a key olfactory cue in locating suitable host plants in several Scolytinae and also Platypodinae species, but usually in less-aggressive species, which use to colonize stressed hosts (Elliott et al., 1983; Cavaletto et al., 2021). Scolytinae species that most frequently attack live trees, and which tend to me more aggressive, hardly respond to ethanol (Miller & Rabaglia, 2009; Kendra et al., 2014; Rabaglia et al., 2019; Mendel et al., 2021), which is the case also for the platypodine *P. quercivorus* (Tokoro et al., 2007). *M. mutatus* fits perfectly in this scenario, as an aggressive species that attacks live trees (Santoro, 1957, 1963; Alfaro et al., 2007).

In our traps baited with the *M. mutatus* sex pheromone blend, 90% of trapped *M. mutatus* beetles were females. These results match with information from the literature, where in Italy on average 90% of trapped beetles were females (67 - 100%; n = 9) (Gonzalez-Audino et al., 2013). The trapping of specimens of the 'non-targeted-sex' (males, in this case) in sex pheromone-baited traps is not uncommon (Borden & Stokkink, 1973; Hager & Teale, 1996; Miller et al., 2000; Allison et al., 2013). The most plausible explanation for this behavior is that these males might be using the male-produced sex pheromone as a cue to locate a suitable host (Chemnitz et al., 2020), or even a female (Müller & Eggert, 1987).

Overall, it appears that *M. mutatus* has a preference for large diameter trunk trees as a function of its spatial gallery pattern and the large brood number each founder female originates. Attacks were concentrated in the lower portion of tree trunks, below 2 m, perhaps because in this part of the trunk the highest diameters are found. The lack of an aggregation pheromone, which seems to be the rule in larger species, which typically attacks live healthy trees, might be the explanation for the fact that few attacks are found per tree. Gummosis was the main factor in African mahogany resistance against attacks from *M. mutatus*, and probably there is a toxicity component of the exuded gum that is also involved in the high observed mortality. In the study area, *M. mutatus* proved to show a multivoltine behavior, but it is expected to be univoltine in colder regions of the country. Ethanol failed to attract *M. mutatus* specimens, probably due to the fact that aggressive species do not respond to kairomones typically released from stressed trees. It is to be determined if other host-specific compounds might be involved in the primary attraction by pioneer beetles to host trees, or if host selection is at random. The sex-pheromone blend attracted, as expected, a majority of females, but some males were attracted as well, and this might indicate that these were using the pheromone cue to help either locating suitable hosts or conspecifics for mating purposes.

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