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Research Article

Sustainability of Mahogany Production in Plantations: Does Resource Availability Influence Susceptibility of Young Mahogany Plantation Stands to *Hypsipyla robusta* Infestation?

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Hypsipyla robusta Moore (Lepidoptera: Pyralidae), like many other moth species, shows selectivity when choosing host plants for its eggs. Four Meliaceae species (*Khaya grandifoliola*, *K. ivorensis*, *Swietenia macrophylla*, and *Entandrophragma cylindricum*) were established in a moist semideciduous forest in Ghana to study this selectivity at 12 and 21 months after planting. The analysis of variance (ANOVA) at a *P*-value of 0.05 was used to test the significance of differences in infestation by *H. robusta* between the species. *H. robusta* attacks were recorded by month 12 after planting in the field, and only *Khaya* spp. was attacked, with attacks evident on 15.5% of *K. grandifoliola* and 6.6% *K. ivorensis*. Saplings in blocks closer to an older *H. robusta* infested *K. grandifoliola* stand had more infestation compared to saplings further away. The mean percentage of *K. grandifoliola* attacked was 38.9%, 38.9%, 13.3%, and 7.4% in 4 different plots located increasingly further away from the older infested plantation. A similar trend was found in *K. ivorensis* with 28.4%, 7.1%, 0.0%, and 0.0% in the plots located increasingly further away from the infested stand. These results indicate a higher number of shoot borer attacks at the edge of the plantation and in proximity to other infested plantations. After 21 months, the fastest-growing species and the fastest-growing individuals within the species were the most infested. *K. grandifoliola* recorded the fastest growth and most attacks followed by *K. ivorensis* and *S. macrophylla*. *E. cylindricum* recorded the least growth and no *H. robusta* infestation. After 21 months, the mean percentages of trees attacked were 59.1%, 23.7%, 5.6%, and 0.0% for *K. grandifoliola*, *K. ivorensis*, *S. macrophylla*, and *E. cylindricum*, respectively. Within species, the fastest-growing saplings experienced the most attacks. A positive correlation was observed between the plant size and *H. robusta* attacks ($R^2 = 0.76$). Attacks resulted in the death of the apical shoot and the proliferation of multiple shoots in only the *Khaya* spp., with *K. ivorensis* recording a lower number of shoots than *K. grandifoliola*. These proliferated shoots were also attacked, and a positive correlation was observed between the number of proliferated shoots and *H. robusta* attacks ($R^2 = 0.84$). These findings will assist plantation developers, forest managers, and investors in mahogany plantations to devise integrated pest management strategies to reduce the impact of *Hypsipyla* attacks on their plantations.

1. Introduction

The *Hypsipyla* (Lepidoptera: Pyralidae) shoot borers cause significant damage to high-value timber species of the Meliaceae and Verbenaceae families. The two most important *Hypsipyla* species are *Hypsipyla grandella*, which occurs in the Neotropics, and *Hypsipyla robusta*, which

occurs throughout tropical Africa, Asia, and the Pacific region, including Australia [1]. *H. grandella* attacks species from the genera *Cedrela*, *Swietenia*, and *Toona* in the Neotropics. *H. robusta*, on the other hand, is reported to attack *Carapa procera*, *Khaya anthotheca*, *K. ivorensis*, *K. grandifoliola*, *K. senegalensis*, *Entandrophragma angolense*, *E. candolei*, *E. cylindricum*, *E. utile* (all African

mahoganies), and *Lovoa trichiloides*; native to tropical Africa and *Chukrasia tabularis*, *Toona* spp. (*T. australis*, *T. ciliata*); native to Asia and Australia, respectively [2–5].

The main damage caused by *Hypsipyla* spp. is inflicted by the larvae, which destroy the principal terminal shoot by boring into the tips and tunneling in the stems of young saplings [4–7]. The larvae of *Hypsipyla* feed on the soft tissue inside the stem. This results in heavy sap exudation, which can lead to killing the main stem [4]. The new shoots that grow in response to shoot borer attacks are also attacked repeatedly by the larvae, and they result in the development of multiple side branches and poorly formed trees, which are undesirable for timber production [6, 8–10]. Attacks by *Hypsipyla* are usually more severe on the stands growing in full sun, and hence, the biggest effects are observed in young plantations, and especially those in monocultures [11–13]. Saplings growing under shade suffer far less damage [12] but at the expense of vigorous growth associated with mahoganies. The control of *Hypsipyla* shoot borers has proven unsuccessful despite significant research and management efforts, which have employed biological, chemical, and silvicultural methods [14–16].

The feeding habits of some insects exhibit a pattern where the host plants located at the boundary of a forest plantation of the same family are attacked more than those in the interior [17]. Darko [18] predicted that the closeness of *H. robusta* insect colonies to a host plant stand might influence the susceptibility of the stand to attacks. However, information on the pattern of attacks in relation to the edge effect is very limited. In earlier studies of species in the *Khaya* and *Entandrophragma* genera, *H. robusta* showed a higher affinity for the *Khaya* species [12, 19].

Female shoot borers are attracted to fast-growing individuals when searching for oviposition sites as they may have more growing shoots available [20], some of which may be succulent and thick enough to ensure the survival and better performance for the larvae. *Hypsipyla robusta* is reported to exhibit this selectivity even when choosing among different individuals of the same species as the host [21]. It could explain why faster-growing mahoganies, especially those in the open field plantations, usually have higher infestation rates than those in the shade or those that are slower-growing species [12, 22].

We examined the pattern of *H. robusta* attacks on four Meliaceae species (*Khaya grandifoliola*, *Khaya ivorensis*, *Swietenia macrophylla*, and *Entandrophragma cylindricum*) in relation to their size, availability of shoots or resources, and the closeness of stands to an *H. robusta* infested *K. grandifoliola* stand in the moist semideciduous forest of Ghana. It was our expectation that the findings could be used to develop strategies for managing *Hypsipyla* in young mahogany plantations.

2. Materials and Methods

2.1. Species, Study Site, and Establishment of Plots. This study was located in the moist semideciduous forest type [23] of Ghana's Upper Guinean tropical forest. This forest type is favorable for the growth of all native West African

mahogany species [23, 24]. The annual precipitation ranges between 1200 and 1750 mm per annum, with a dry season from December to March with a rainfall of less than 100 mm per month. All experiments were established at the Forestry Research Institute of Ghana (FORIG) Mesewam nursery and research center near Kumasi.

The four study species are *K. grandifoliola*, *K. ivorensis*, *E. cylindricum*, and *S. macrophylla*. Twelve seedlings of each of the four species (treatments) were planted per plot at a spacing of 2 m × 2 m. Each species (treatment) was replicated four times in a randomized block design. All the plots used were weeded regularly to reduce competition with weeds and also for easy access during data collection. No other silvicultural manipulations were carried out on any of the plots during the period of monitoring.

2.2. Data Collection. For each of the four species (*K. grandifoliola*, *K. ivorensis*, *E. cylindricum*, and *S. macrophylla*), data were collected 12 and 21 months after planting. The total height was measured from the stem base of each plant to the tip of the leading shoot, and the height of the clear trunk (height to the first fork) was measured from the base of the plant to the base of the first branch [25]. The diameter of each plant was measured 10 cm above the ground [26].

We assessed *H. robusta* attacks by visually inspecting each plant for the presence of frass and dieback with or without the development of new or multiple shoots. The total number of shoots growing per plant was counted along with the number of shoots attacked per plant [12, 27].

2.3. Data Analyses. Data collected for each species were grouped into *H. robusta*-attacked and -nonattacked saplings, and the relationships established were as follows:

- (a) Plant size (mean height, diameter, and height at the first fork) of *H. robusta*-attacked and -nonattacked saplings for each of the four species
- (b) Mean shoots proliferated per plant and mean shoots attacked per plant
- (c) The influence of the proximity of plots to an older *H. robusta* infested *K. grandifoliola* plot

The means of the data were calculated, and overall differences among the species (treatments) were tested using the analysis of variance (ANOVA) at a *P*-value of 0.05, followed by Tukey's test (Post hoc test) to compare treatment pairs. Analyses were conducted using Statistixl [28] and Graphpad Prism 5 software [29] (<http://www.statistixl.com>; <http://www.graphpad.com>). The relationships between variances and means were compared, and where necessary, the data were transformed.

3. Results

3.1. Relationship between Saplings/Plant Size and Incidence of Attack. The data collected on the 4 species and analyzed twelve months after planting in the field showed significant

differences ($P = 0.041$) in *H. robusta* attack among the species, as only the *Khaya* species had recorded attacks with a mean percentage of 15.5% of *K. grandifoliola* and 6.6% of *K. ivorensis* trees attacked (Table 1). The mean height and diameter of the attacked saplings were greater than those that were not attacked within each species (Figures 1(a) and 1(b)). This trend was again evident 21 months after planting in the field. However, the mean height of the attacked trees was 1.46 m, 1.25 m, and 1.79 m for *K. grandifoliola*, *K. ivorensis*, and *S. macrophylla*, respectively, and the mean heights of the nonattacked individuals were 1.11 m, 0.85 m, and 1.05 m for *K. grandifoliola*, *K. ivorensis*, and *S. macrophylla*, respectively (Figures 2(a) and 2(b)). At the end of the 21st month, *S. macrophylla* had also been attacked by *H. robusta* (Table 1), and the mean percentages of trees attacked were 59.1%, 23.7%, 5.6%, and 0.0% for *K. grandifoliola*, *K. ivorensis*, *S. macrophylla*, and *E. cylindricum*, respectively, and they varied significantly ($P = 0.000$). The same trend was observed, whereby the mean height and corresponding diameters of the attacked saplings recorded higher values than those of the nonattacked saplings (Figures 2(a) and 2(b)).

3.2. Height of Clear Trunk and the Relationship between Average Shoots Developed and Shoot Attacked. The number of shoots sprouted on the attacked saplings of each species was generally higher than the number on nonattacked saplings. It was also significantly higher for all the species at 12 and 21 months with the exception of *K. grandifoliola* at 12 months (Figure 3). In the 12th month, when the attack was first observed in *K. ivorensis* and *K. grandifoliola*, their mean shoots per sapling was 1.1 and 1.26, respectively, while the other two species (*S. macrophylla* and *E. cylindricum*) recorded an average of 1.0 leading shoot per plant (Table 2). Twenty one months after planting in the field, *K. grandifoliola*, *K. ivorensis*, and *S. macrophylla* had 4.3, 3.0, and 4.0 mean sprouted shoots in response to *Hypsipyla* attacks, while the nonattacked trees had 2.1, 1.5, and 1.2 mean shoots for *K. grandifoliola*, *K. ivorensis*, and *S. macrophylla*, respectively. The percentage of shoots that were attacked varied among the species. *Entandrophragma cylindricum* recorded a 0% shoot attack for the entire data collection period, while *S. macrophylla* recorded only 2.8% shoot attack in the 21st month. *Khaya ivorensis* recorded 27.1% and 44.0%, while *K. grandifoliola* also recorded 47.0% and 44.9% shoots attack for the 12th and 21st months, respectively (Table 2).

With reference to the attacked and nonattacked trees, the height of the clear trunk was greater for the attacked trees. For each species on each measurement date, the difference in the height of the clear trunk between the attacked and nonattacked trees was significant ($P < 0.05$), with the exception of *K. grandifoliola* at month 12 (Figure 4). The mean height of the clear trunk recorded was 0.88 m, 0.88 m, and 0.99 m for the attacked *K. grandifoliola*, *K. ivorensis*, and *S. macrophylla*, respectively, compared with 0.65 m, 0.66 m, and 0.41 m for the nonattacked *K. grandifoliola*, *K. ivorensis*, and *S. macrophylla*, respectively.

The attacks of the leading shoots as observed in the 12th month led to the proliferation of multiple shoots, which were also subsequently attacked. The regression equation between the shoot attacked on the total shoots developed by each sapling showed a positive relationship for *K. ivorensis* ($R^2 = 0.76$) and *K. grandifoliola* ($R^2 = 0.84$) (Figures 5 and 6). The relation was developed for only *K. ivorensis* and *K. grandifoliola* since they recorded significant attack levels and subsequently developed multiple shoots.

3.3. Proximity to Infested Plots as a Factor for Sapling Infestation. Twelve months after planting, it was observed that the saplings in the blocks closer to a four-year-old *K. grandifoliola* stand recorded higher levels of attack. Block 1 was the closest to the older *K. grandifoliola* stand, followed by blocks 2, 3, and 4 (Figure 7). The percentage of saplings attacked in blocks 1, 2, 3, and 4 for the *Khaya* species, which were the only attacked species in month 12, was the highest in block 1, and it decreased from blocks 2, 3, and 4, respectively (Table 3). None of the saplings of *E. cylindricum* and *S. macrophylla* arranged in the blocks of the Meliaceae species trial was attacked 12 months after planting. Hence, a proximity effect was not evident.

4. Discussion

4.1. Relationship between Sapling/Plant Size and Incidence of Attack. Data collected at the end of 12 and 21 months were regrouped into the attacked and nonattacked saplings for each of the four species. The three species *K. ivorensis*, *K. grandifoliola*, and *S. macrophylla* had some of their saplings attacked in this study and showed similar trends. The attacked saplings were relatively taller and bigger than the nonattacked ones, which were shorter and smaller and corroborated the vigor hypothesis [30]. Cunningham and Floyd [31] and Mo et al. [20] also reported a similar trend of positive correlation between *Hypsipyla* attacks and plant size in *Toona* species. *Khaya grandifoliola* was the fastest and the tallest growing among the four Meliaceae species, which could have contributed to its saplings being more attractive to and preferred by *H. robusta*, thereby resulting in its saplings experiencing more attacks than the other species [22, 31, 32].

Female insects are attracted to fast-growing trees because they have more growing shoots available [20], some of which may be thick. *Hypsipyla* may prefer to oviposit on the thick succulent shoots [22, 33], probably as a means of ensuring the survival of its progeny [34]. In the field and laboratory experiments, insects tend to be attracted to the shoots and leaves of relatively fast-growing trees than those of the slow-growing ones [22, 34, 35]. It may explain why saplings that were attacked were relatively tall and big.

Although not examined in this study, the attractiveness of a tree to the insects is usually based on the nutritional value of the plant [22], which, according to Heisswolf et al. [34], is very high in larger (fast-growing) trees than the smaller ones. It may be attributed to changes and/or increases in the production of certain chemicals in these faster-growing species in the open, which may affect the signal that

TABLE 1: Percentage of *K. grandifoliola*, *S. macrophylla*, *K. ivorensis*, and *E. cylindricum* saplings attacked in the species trial after 12 and 21 months in the moist semideciduous forest.

Treatment	Percentage of saplings attacked (%)	
	12 months	21 months
<i>K. ivorensis</i>	6.607 ^a ± 5.482	23.686 ^a ± 6.193
<i>K. grandifoliola</i>	15.483 ^a ± 5.194	59.060 ^b ± 11.954
<i>E. cylindricum</i>	0.000 ^a ± 0.000	0.000 ^a ± 0.000
<i>S. macrophylla</i>	0.000 ^a ± 0.000	5.556 ^a ± 5.556
<i>P</i> values	0.041	0.000

Values are percentages, and ± are standard errors. Percentages in the same column with the same letter are not statistically different at *P* value of 0.05. Differences between means were compared using Tukey's test (Post Hoc tests).

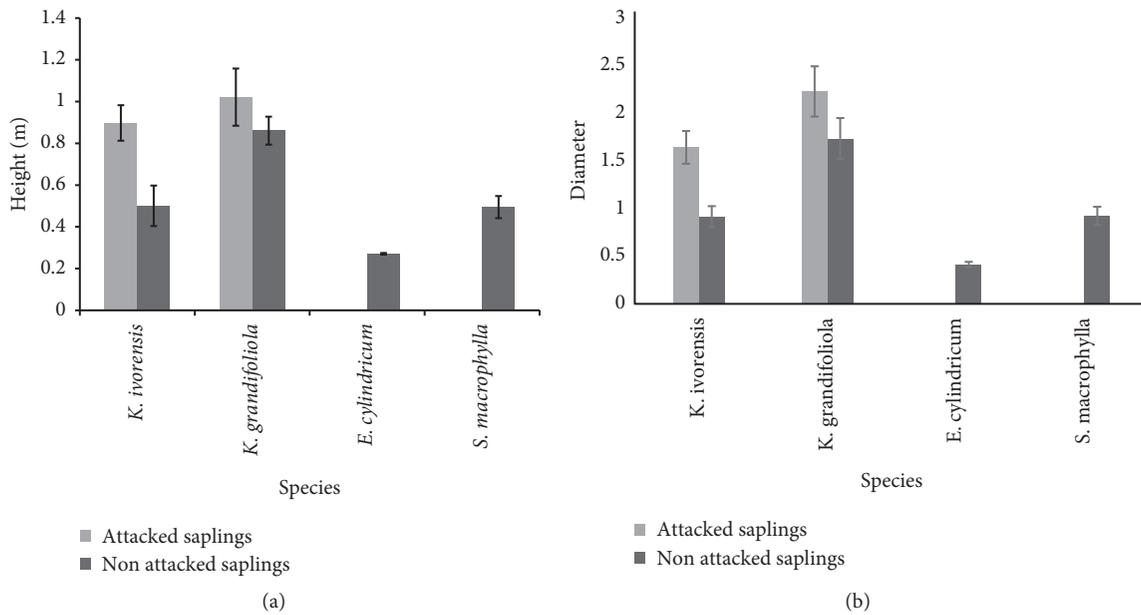


FIGURE 1: Mean height (a) and diameter (b) of the attacked and nonattacked saplings of the four Meliaceae species 12 months after planting.

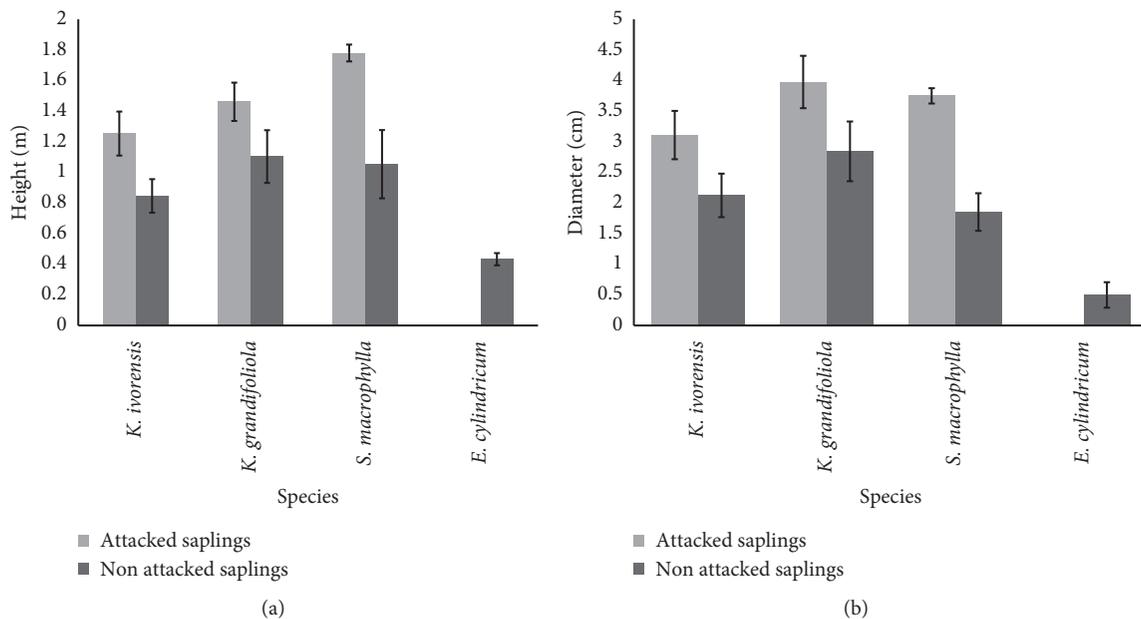


FIGURE 2: Mean height (a) and diameter (b) of the attacked and nonattacked saplings of the four Meliaceae species 21 months after planting.

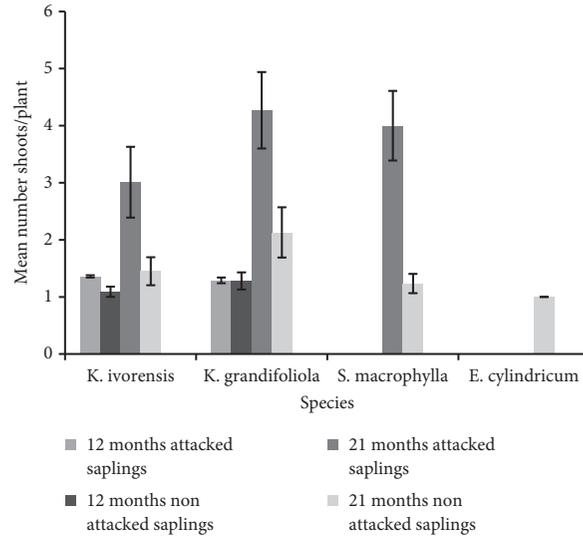


FIGURE 3: Mean number of shoots on the attacked and nonattacked saplings of the four Meliaceae species 12 and 21 months after planting in the moist semideciduous forest.

TABLE 2: Mean shoots and percentage shoots attacked for *K. grandifoliola*, *S. macrophylla*, *K. ivorensis*, and *E. cylindricum* in the species trial 12 and 21 months after planting in the moist semideciduous forest.

Treatment	Mean shoots		Percentage of shoots attacked (%)	
	12 months	21 months	12 months	21 months
<i>K. ivorensis</i>	1.100 ^a ± 0.019	2.056 ^a ± 0.352	27.120 ^a ± 19.581	43.955 ^a ± 10.432
<i>K. grandifoliola</i>	1.257 ^b ± 0.052	3.859 ^b ± 0.342	47.040 ^a ± 11.905	44.898 ^a ± 8.752
<i>E. cylindricum</i>	1.000 ^a ± 0.000	1.000 ^c ± 0.000	0.000 ^a ± 0.000	0.000 ^b ± 0.000
<i>S. macrophylla</i>	1.000 ^a ± 0.000	1.000 ^c ± 0.000	0.000 ^a ± 0.000	2.750 ^b ± 2.750
P values	0.000	0.000	0.035	0.000

Values are percentages, and ± are standard errors. Percentages in the same column with the same letter are not statistically different at P value of 0.05. Differences between means were compared using Tukey’s test (Post Hoc tests).

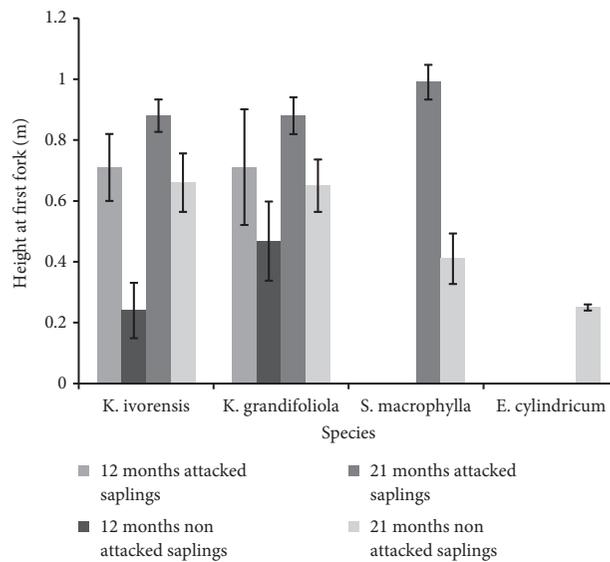


FIGURE 4: Mean height to the first fork of the attacked and nonattacked saplings of the four Meliaceae species 12 and 21 months after planting in the moist semideciduous forest.

attracts the adult lepidopterans for oviposition [22, 34]. Mahroof et al. [22] further suggested that if antifeedants indeed exist in mahoganies, then they may be inactive or absent during the early flushing of leaves since this is the

period of intense attack. Slow-growing plants, on the other hand, are woodier, have poor quality resources and low nutritional value for larvae development [36], and may be fortified with antiherbivory chemicals.

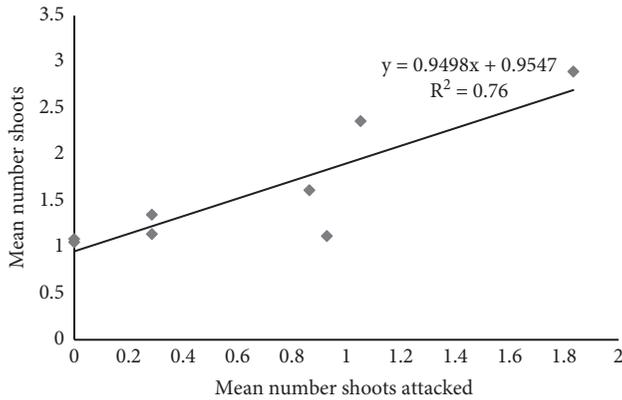


FIGURE 5: Relationship between the mean number of shoots and the mean number of shoots attacked for *K. ivorensis* in the species trial 21 months after planting in the moist semideciduous forest.

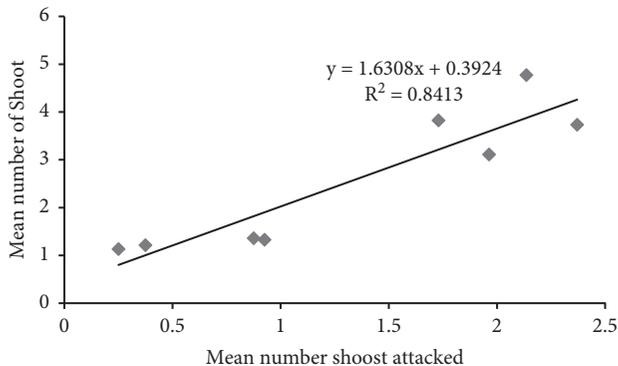


FIGURE 6: Relationship between the mean number of shoots and the mean number of shoots attacked for *K. grandifoliola* in the species trial 21 months after planting in the moist semideciduous forest.

4.2. Height of Clear Trunk and the Relationship between the Average Shoots Developed and Shoots Attacked. The Meliaceae often produce an average of one leading shoot per plant in the absence of *Hypsipyla* attacks [12]. Eight months after planting, observations indicated that none of the species was attacked, and the number of shoots per sapling was one. With the onset of attack that resulted in the death of the apical dominant shoot [26, 32] by the 12th month in general, both *Khaya* species had the mean number of shoots sprouted to be 1.1 and 1.3 for *K. ivorensis* and *K. grandifoliola*, which increased to 2.1 and 3.9, respectively, in the 21st month. These sprouting shoots were considered a suitable substrate for egg deposition and the development of larvae of the *Hypsipyla* moth [37] and were also attacked. Hence, a positive linear relationship between the shoots attacked and the total shoots of *K. grandifoliola* and *K. ivorensis* was observed in the trial.

The number of shoots recorded for the attacked saplings of *K. grandifoliola*, *K. ivorensis*, and *S. macrophylla* at the end of the 21st month was more than double that was recorded in the 12th month. It suggests that as new shoots are sprouting as a result of attacks, the new shoots also get attacked, causing more shoots to develop, thereby increasing the availability of resources

[20] that may be suitable for *H. robusta* to feed on or attack. Similar results have been reported for *Toona ciliata*, which is also in Meliaceae [38]. *Entandrophragma* spp. had no attacks, and thus they generally had a single shoot that conformed to the observations made by Opuni-Frimpong et al. [3]

The significantly greater height of the clear trunk recorded by the attacked saplings could be attributed to the attacked saplings showing some level of recovery after the attacks by shedding off the old branches. The increase in the mean height of the clear trunk for *K. grandifoliola* was lower than that of *K. ivorensis* from the 12th to the 21st month (Figure 4). It could be attributed to the high number of shoots developed after the attack and what Opuni-Frimpong et al. [12] referred to as self-pruning. Self-pruning was observed in the *K. grandifoliola* but was less pronounced and similar to the observations made in *K. anthotheca* [12].

Khaya ivorensis, on the other hand, developed an average of two shoots per sapling, of which only one shoot was attacked. These relatively few sprouted shoots in response to *H. robusta* attacks together with self-pruning (which was more pronounced and a major characteristic associated with *K. ivorensis*) could have contributed to the better recovery and higher clear trunk observed in *Khaya ivorensis* [12].

Some researchers have considered self-pruning as a means of showing resistance or tolerance to *Hypsipyla* attacks [3, 39]. Self-pruning, together with artificial pruning, could be used as a silvicultural tool to increase the bole length of the Meliaceae to the 8–10 m height, which is sought for merchantable boles [6, 25].

4.3. Proximity to Infested Plots as a Factor for Sapling Infestation. The experimental plot used to conduct this trial lies opposite to a forest used for research purposes, with block 1 immediately opposite to it (Figure 7). Adjacent to that forest on both sides were three- and four-year-old *Khaya grandifoliola* research plots, which have experienced *H. robusta* attacks. These infested plots may have been the sources of *H. robusta*, which attacked the Meliaceae species in this study. The closeness of a food source to an insect colony may determine how fast the food source is attacked by the insect. It could explain the blocking effect observed, where the blocks (1 and 2) that were closer to the old *K. grandifoliola* stands experienced higher levels of attack than those further away but on the same plot (blocks 3 and 4) in the 12th month. The observation conforms to that made by Darko [18] when *K. grandifoliola* was studied in a mixed plantation and agroforestry setting in the same location. The observation also shows a positive response of initial *H. robusta* attacks to the edge effect in the Meliaceae species trial [17]. *E. cylindricum* and *S. macrophylla* were not attacked even though they were arranged in the same blocks in the Meliaceae species trial, which could be attributed to the preference of *H. robusta* to *Khaya* species [3]. This pattern was not maintained as attack levels generally increased in the *Khaya* species on the 21st month, where *S. macrophylla* recorded its first attack.

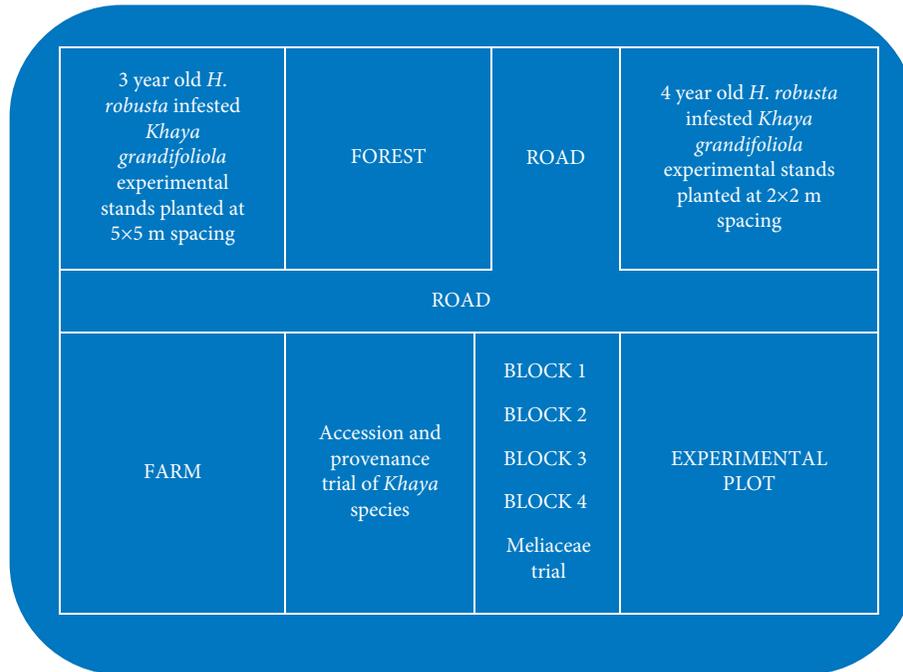


FIGURE 7: Schematic layout of the trial sites for the Meliaceae species blocks.

TABLE 3: Percentage of saplings attacked by *H. robusta* in various blocks of the Meliaceae species trials in the moist semideciduous forest types in the 12th month.

Accessions/species	Attacked saplings (%)			
	Block 1	Block 2	Block 3	Block 4
<i>K. ivorensis</i>	28.36	7.14	0.00	0.00
<i>K. grandifoliola</i>	38.88	38.88	13.33	7.41
<i>S. macrophylla</i>	0.00	0.00	0.00	0.00
<i>E. cylindricum</i>	0.00	0.00	0.00	0.00

5. Conclusions

We examined the pattern of *H. robusta* attack on four Meliaceae species (*Khaya grandifoliola*, *Khaya ivorensis*, *Swietenia macrophylla*, and *Entandrophragma cylindricum*) in relation to the plant size, availability of shoots or resources, and proximity to an *H. robusta*-infested *K. grandifoliola* stand in the moist semideciduous forests of Ghana.

- (i) The closeness of a young plantation to an already established plantation with *H. robusta* infestation may increase their vulnerability to attack, with saplings closer to the infested stands experiencing initial attacks.
- (ii) Faster growing and taller saplings of each species were attacked more than the slower growing saplings.
- (iii) *Hypsipyla robusta* infestation leads to the proliferation of multiple shoots, providing resources for further attacks and branching. The more the proliferations of the shoots, the more the shoots attacked.

- (iv) Saplings show recovery by the increase in the height of clear trunk over time.

Our results provide insight for further efforts aimed at developing strategies to restore mahogany species in forest landscapes in the tropics.

Data Availability

The data used to support this study will be made available upon request to the corresponding author by any one who needs it.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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