

Impacts of forest pests on wood production in *Khaya senegalensis* plantations established in three climatic regions of Benin

Akotchiffor Kevin Geoffroy
DJOTAN
Kenji FUKUDA

Laboratory of Forest Sciences, University of Abomey-Calavi, Cotonou, Benin
Laboratory of Forest Botany, University of Tokyo, Tokyo, Japan

Norihisa MATSUSHITA

Laboratory of Forest Botany, University of Tokyo, Tokyo, Japan

Augustin Kossi Nounangnon
AOUDJI

Laboratory of Forest Sciences, University of Abomey-Calavi, Cotonou, Benin

Jean Cossi GANGLLO

Laboratory of Forest Sciences, University of Abomey-Calavi, Cotonou, Benin

Empirical data reporting forest pest damage on *Khaya senegalensis* have raised concerns over their potential economic impacts. Although the problem was also reported in Benin, scientific data on their economic impact on plantations are lacking. In this study, we combined dendrometry and survey data to estimate the economic impact of wood damage caused by pests in *K. senegalensis* plantations in Benin. We found that four major pest guilds cause damage to the plantations with severe wood production loss. Wood borers are the most economically damaging guild, mainly in mature plantations, while shoot borers and defoliators predispose trunks to bifurcation and deformation in young plantations. We estimated damage to $8.3 \pm 5.4 \text{ m}^3 \text{ ha}^{-1}$ of wood production, corresponding to an economic loss of $825.5 \pm 635.4 \text{ USD ha}^{-1}$. Our findings suggest that pest management in *K. senegalensis* plantation should focus on the developmental stages and ecological interactions between host and pest to reduce the economic impacts of wood damage.

Keywords: African mahogany, Major pest, Destruction of wood, Economic impact

INTRODUCTION

Forest resources are essential for human well-being (Millenium Ecosystem Assessment, 2005; Bodeker and Burford, 2005; Nair, 2007), but tropical forests are being cleared at an annual rate of 5.5 million hectares (Keenan et al., 2015). Meanwhile, plantations can supplement natural forests by providing essential forest products to reduce forest clearing (Nair, 2007). In these efforts, the number of tropical forest plantations has increased exponentially since the mid-1960s (Nair, 2007; Payn et al., 2015). Likewise, Benin is not staying behind the efforts made worldwide to reduce the impacts of forest exploitation for timbers. One of the native tree species widely planted in Benin is *Khaya senegalensis* (Desv.) A. Juss., or African mahogany. The first plantation of *K. senegalensis* was settled in 1935 (Sokpon and Ouinsavi, 2004). The species is still being used in the reforestation and plantation projects have taken place over the last 15 years in Benin (Akpona et al., 2016).

K. senegalensis is a high-value hardwood species (Sokpon and Ouinsavi, 2004). Unfortunately, some economically threatening mahogany shoot borers, such as *Hypsipyla robusta* Moore (Newton et al., 1993) and *Hypsipyla grandella* Zeller (Zanetti et al., 2017), severely attack the tree in established plantations (Floyd, 2001; Sokpon and Ouinsavi, 2002; 2004; Opuni-Frimpong et al., 2008). Many

reports (more than 300) from studies carried out under the tropics have highlighted severe damage to mahogany shoot borers. They have raised concerns over the potential setbacks on *K. senegalensis* plantations (Griffiths, 2001). For example, damage to *K. senegalensis* by boring insects and caterpillars in Benin has been reported (Sokpon and Ouinsavi, 2002; 2004).

When they occur, insect attacks can severely impact the value of the timber (Opuni-Frimpong et al., 2008). Reported patterns of damage range from perforation of young apical shoots to tree bifurcation (Floyd, 2001; Nair, 2001; Sokpon and Ouinsavi, 2002; 2004). Attacks occur predominantly in monoculture plantations (Nair, 2001), lead to high mortality rates (Botha et al., 2004), alter the engineering qualities of the wood (Griffiths, 2001; Nair, 2001; 2007; Sokpon and Ouinsavi, 2002), and cause significant economic damage (Griffiths, 2001). To help avoid or reduce injuries induced by pests, mainly *H. robusta*, Djotan et al. (2018) modeled the ecological niche of the host (*K. senegalensis*) and pest (*Hypsipyla robusta*) to identify vulnerable zones in West Africa. To date, there are not, however, any previous studies that described the pest guild associated with damage to the plant or estimated the economic impacts related to attacks on the wood in planted stands of *K. senegalensis* in Benin.

We surveyed three *K. senegalensis* plantations in Benin and interviewed neighboring populations to describe damage to the tree, specifically the wood, and estimate the related-economic losses. Finally, we discussed the ecological and biological interactions between the tree and the damage-associated pest guild.

MATERIAL AND METHODS

Khaya senegalensis

K. senegalensis is referred to as “Cailcédrat” or “Acajou d’Afrique” in French, “African Mahogany” or “Dry zone Mahogany” in English, and “Acao” in Fon, a local, national dialect of Benin. It is native to 20 West African countries, including Benin (Nikiema and Pasternak, 2008; Orwa et al., 2009). It is a semi-deciduous tree species that does not tolerate shade (Sokpon and Ouinsavi, 2002). It is found in various vegetation types, including gallery forests, dry, dense forests, woodland forests, and savannahs in the Sudano-Guinean and Sudanian ecological regions of Benin (Sokpon and Ouinsavi, 2002).

Study sites

The study was carried out in the West African nation of Benin. Benin extends from a latitude of 6°14' to 12°25' North and a longitude of 0°46'E to 3°51' East (DIVA-GIS, 2018). It spans three climatic zones, ranging from humid to semi-arid (Sinsin et al., 2004): the Guineo-Congolese zone (humid), the Sudano-Guinean transition zone (sub-humid), and the Sudanian zone (semi-arid) (White, 1986). We surveyed three *K. senegalensis* plantations in the three climatic zones in Atcherigbe, Toffo, and Tanguieta villages (Figure 1). In Toffo and Atcherigbe, *K. senegalensis* stands are in the reforestation perimeter of the Lama and Atcherigbe forest reserves. However, the *K. senegalensis* stand in Tanguieta is a patch of an urban forest.

Stand survey

At each plantation, the sample size (the number of observed trees) was determined following (Dagnelie 1998). We observed, described, and measured 297 *K. senegalensis* trees (Table 1). Within each plot, the diameter at breast height (DBH) of all individuals was measured. The tree height and stem height were measured and used to calculate the ratio of tree height to stem height. The crown size (crown diameters) of all individuals was measured using diameter measuring tapes and a SUUNTO clinometer following Preuhlsler (1981) to calculate the quadratic mean crown diameter following Pretzsch et al. (2015). We recorded the attacks observed on the trees and the damage to

the wood by visually estimating the proportion of lost timber. The accessible parts of the entire tree were examined, including bark, branches, leaves, and shoots. We also recorded the deformation status of every investigated tree.

Interviews with plantation neighbors

We conducted a total of 85 interviews with neighbors of the surveyed plantations (Table 2). The interviewees comprised forest workers, plantation owners, farmers, forest officers, carpenters, and wood traders. The National Office of the Woods of Benin (ONAB) and the General Department of Waters, Forests, and Hunts of Benin (DGEFC), which jointly manage the surveyed plantations, recommended potential interviewees known to have sufficient knowledge of the subject. We randomly selected the first interviewee in each region from the pool and then used the snowball method to identify and question other interviewees. We used questionnaires to record interviewees' knowledge of forest pests that negatively impact the growth of *K. senegalensis* or the engineering quality of its wood. We asked questions about our observations in the plantations, the market value of destroyed wood compared to non-destroyed wood, and the time of year and stage of plant development (expressed as tree age) when infestations start or are prominent.

Data analyses

Description of the damage to the trees

We summarized and presented survey and interview data as histograms and bar plots. We used the χ^2 proportion test on the size-class structures of DBH, tree height, stem height, the ratio of tree height to stem height, and crown diameter to test the null hypothesis that the proportion of attacked trees across classes of a variable, regardless of the type of pest that initiated the attack (probabilities of attack), was equal. In addition, we used the χ^2 test of independence to check the variation in attacks and the link between stem deformation and the status of attacks. At the all-sites level, only the ratio of the tree height to the stem height and the crown diameter were tested with the χ^2 proportion test to clarify any dependence of attacks on the crown shape.

Wood loss and economic impact related to damage on the trees

Stem volume was computed using a model specific to *K. senegalensis* (Eq. 1) built by Goussanou et al. (2016):

$$\ln(V) = -1.90 + 1.89 \cdot \ln(D) + 0.62 \cdot \ln(H) \quad (\text{Eq. 1})$$

Where V is the stem volume (10-3 m³), D is the diameter at breast height in cm, and H is the stem height in m. The attack rate ($R\%$) in each stand was calculated by dividing the number of attacked trees by the total number of trees. The average percentage of lost wood on damaged trees (Prop loss_stem) was computed from observational data of Tanguieta and Toffo. The R and Prop loss_stem product was used to estimate the average proportion of stand wood loss (Prop loss_stand). In the stands of Tanguieta and Toffo, the average wood volume in cubic meters per hectare within each plot ($V_{\text{Wood_plot}}$) was computed using *K. senegalensis* species-specific models (Eq. 2). Then the average values were computed for each stand ($V_{\text{Wood_stand}}$) (Eq. 3).

The volume of lost wood per hectare ($V_{\text{loss_stand}}$) was computed by multiplying the average proportion of wood production loss per stand (Prop loss_stand) by the average stand wood production ($V_{\text{Wood_stand}}$) as in (Eq. 4):

In (1-3), s is the plot area in ha, H is the stem height in m, and D is the DBH in cm. All parameters were computed with 95% confidence intervals.

The price of a cubic meter of lumber was used to estimate the economic loss incurred by damage

on *K. senegalensis*. Price distributions reported by interviewees were described using box and whisker descriptive statistics, and mean values were compared using the Kruskal-Wallis rank-sum test. The same test was performed to analyze the variation in reported prices among respondents' socio-professional groups. The value of a cubic meter of lumber was used to estimate financial losses from pest damage on mature *K. senegalensis* stands (Eq. 5) in French Colonies Currency per hectare (XOF ha⁻¹), which we converted into United States Dollar per hectare (USD ha⁻¹) using the conversion rate USD XOF-1 = 0.0017000 (The Money Converter 2019).

RESULTS AND DISCUSSION

Knowledge of the interviewees on pest occurrence in *K. senegalensis* plantations

Interviewees' reports revealed that pests attack all parts of the trees regardless of age and mostly during rainy seasons (Figure 2a-c). In addition, most of the interviewees have informed that leaves and wood are frequently attacked (Figure 2a). Their knowledge was relevant to the plantations surveyed in this study and more broadly related to the subject. They reported that infestations begin about two years after planting (Figure 2), which agrees with previous findings where infestation rates were higher during the initial phases of plant development (Ennion, 2003). Infestations can reach 70% in the first year after planting and up to 100% after two years (Paul and Weber, 2013). A wide range of tree ages is attacked (Figure 2), indicating that trees can be attacked anytime if environmental conditions are suitable. Infestations occur, or are most noticeable, from June to August (Figure 2). This report follows (Zanetti et al., 2017), who reported that pests can attack plants at any time and that one larva per plant is enough to cause significant damage. All parts of the trees are attacked (Figure 2), particularly the leaves, and attacks occur on young and old trees.

Damage to *K. senegalensis* trees in the plantations

We observed attacks on leaves, stems, trunks, branches, bark, wood, and roots and identified four pest guilds: shoot borers and defoliators, wood borers, termites, and saprophytic fungi (Figure 3). The damage they induced on *K. senegalensis* includes wood bumps and scabies; holes across the bark and into the wood; deformed trunks and stems; perforated, folded, stained, and discolored leaves; insect reproduction under the bark; and wood rot. Saproxyllic beetle pupae were found in the phloem, cambial zone, and young xylem of mature trees. The internal and external wood of the trees were destroyed by termites, whose activities are sometimes supplemented by saprophytic fungi. Our observational data revealed more infestations on the leaves in Atcherigbe but almost none in Toffo and Tanguieta, which may be due to the inability to observe infestations on the leaves located beyond our sight. Because interviewees are users of the biomaterials of *K. senegalensis*, their reports may generally be more reliable than our one-time observations.

Previous studies and observations have reported *Hypsipyla* caterpillars feeding on the shoots of *K. senegalensis* (Griffiths, 2001; Nair, 2001, 2007; Sokpon and Ouinsavi, 2002). Although we also observed *Hypsipyla* caterpillars, perhaps the same as those observed by Sokpon and Ouinsavi (2002), we cannot be sure which species were observed because we did not perform detailed taxonomic identification. *Hypsipyla robusta* occurs in West and East Africa, Asia, and the Pacific (Griffiths, 2001), while *Hypsipyla grandella* occurs in South America (excluding Chile), Mexico, the Caribbean, Central America, and South Florida. *Hypsipyla* species follow the Meliaceae distribution pattern they feed on (Griffiths, 2001; Nair, 2007). The species are indistinguishable from one another (Griffiths, 2001), and the taxonomy of the genus is not yet clear (Griffiths, 2001; Horak, 2001), making it difficult to confirm whether the caterpillars shown in Figure 3 were *H. robusta* or *H. grandella*. Four primary pest guilds appear to pose economic threats to *K. senegalensis* plantations (Figure 3): *Hypsipyla* caterpillar defoliators, beetle pupae, termites, and saprophytic fungi. Saprophytic fungi decay bark and wood after degradation by termites. Several fungus species are associated with bark beetles because of their parasitic or mutualistic relationships

(Lombardero et al., 2003; Hofstetter et al., 2006). Such fungi make logs worthless (Mathre, 1964; Adams et al., 2009) and contribute to attacked trees' deaths (Mathre, 1964).

Other pests target leaves, stems, trunks, branches, bark, wood, and roots, including beetles, termites, and ants (Figure 3). This occupation of different niches on the trees corroborates the statement that insects can adapt morphologically, physiologically, and behaviorally to feed on almost all parts of a tree by defoliation, feeding on sap and reproductive organs, and boring into shoots, bark, and the sapwood (Nair, 2007).

Effects of environmental and biological factors on the pest attack of *Khaya senegalensis*

The attack rate was lower in the plantation of Toffo than in other plantations (Table 3). We also observed that leaves were more frequently attacked in the young stand (Atcherigbe) while the wood was more regularly attacked in the older stands (Toffo and Tanguieta). Most of the attacked trees had their trunk deformed (Figure 4). The size-class structures of attacked and non-attacked trees revealed different trends across plantations. In Atcherigbe, the probability of an attack did not vary with the classes of diameter, height, or crown size (Figure 5) as it did in Toffo. There, the tallest trees with the largest diameter were attacked the most. Individuals with a lower ratio of tree height to stem height and lower crown diameter were less attacked. In Tanguieta, the probability of an attack did not vary significantly with diameter, height, or crown size. However, the size-class distribution of those variables indicated that shorter trees were attacked more. Considering all three sites, we found that small trees with smaller crown diameters and smaller tree height to stem height were less attacked than those with tall and large crowns.

The variation in pest occurrence across the three investigated plantations may be explained by the age and the size class structure of the plantation. Plantations are in different climatic zones with different environmental conditions, which may also explain the difference in the attack rates observed between plantations. Tanguieta is warmer and dryer than Toffo and Atcherigbe, with one rainy season lasting from May to October and one long dry season lasting from November to May. In Atcherigbe and Toffo, there are two rainy seasons, March through July, and September through November, but Atcherigbe is warmer and dryer than Toffo because of the proximity of the latter to the sea (Adomou, 2005; Neuenschwander et al., 2011). These differences may explain the greater degree of pest damage in Tanguieta. Pest occurrence is common in warm, dry conditions when insect-breeding vegetal debris is available (Phillips, 2002). The risk of an infestation can be magnified by periodic drought conditions (Stone et al. 2012), which are more frequently observed in Tanguieta and Atcherigbe than in Toffo. Pests might also be more sensitive to humidity (Morgan, 1989; Bassett et al., 2011), which varies among the three sites. Investigating more than one plantation per climatic zone would have been more helpful in concluding on the influence of environmental factors on pest attacks in plantations. Still, because trees were observed rather than the plantations in our study, it is relevant to consider the ecological differences in explaining the pest attacks in *Khaya senegalensis*.

The maturity of a stand can affect infestation patterns due to the relative availability of breeding vegetal material, such as wood debris for the construction of galleries under the bark and phloem tissues for feeding and reproduction (Wood, 1982; Erbilgin et al., 2002). Pest occurrence in Tanguieta, Toffo, and Atcherigbe could be the result of a bottom-up control mechanism related to environmental stresses from boring and sucking insects (Chase et al., 2000; Maloney and Rizzo, 2002) or a top-down control mechanism related to the composition and structure of a stand (Carson and Root, 2000; Long et al., 2003; Carson et al., 2008). In the uneven-aged stand with a bimodal size class distribution in Toffo (Figure 5), canopy trees were more frequently attacked than understory trees. This trend was observed by Neumann and Morey (1984) and Neumann (1987), who found that insect pests attack healthier trees when the density of the stand is high. Insect pests may prefer more vigorous trees when resources are abundant. As we observed, attacked trees should produce new shoots to survive when being severely defoliated by caterpillars. However, in the even-aged stands (Tanguieta and Atcherigbe) with a nearly normal-sized class

distribution, the proportion test revealed that the probability of an attack did not vary with classes of studied variables. Nonetheless, understory trees in Atcherigbe were more frequently infested than canopy trees. Erbilgin et al. (2002) reported that secondary pests infest dead, stressed, or unhealthy trees, which describes most infested trees in Atcherigbe.

Damage-related wood loss and economic impact

Interviewees' reports revealed that lumber made from insect-damaged wood was less valuable (58.7 ± 9.47 USD m⁻³) than damage-free wood (99.4 ± 12.1 USD m⁻³). Fifty percent reported that the price of a cubic meter of lumber from damage-free wood ranged from 40 000 to 85 000 XOF (67.8-144.2 USD), while lumber from pest-damaged wood ranged from 20 000 to 50 000 XOF (33.9-84.8 USD). The value of damage-free lumber was then reported to be about 1.7-fold higher than that of damaged lumber (assuming the level of damage did not render the lumber unusable) (Figure 6). Lumber prices reported by interviewees did not vary among the socio-professional groups. The wide range of lumber prices reported by interviewees can be explained by the inversely proportional relationship between price and the extent of the damage. All interviewees had the same opinion on pests and their economic costs. Therefore, the considerable variation in the reported price of a cubic meter of lumber per category (Figure 6) cannot statistically impute the difference in their socio-professional activities (the Kruskal-Wallis rank-sum test probability was higher than 0.05). Most interviewed farmers (70%) could not estimate the price of a cubic meter of damaged wood compared to damage-free wood, suggesting that they know *K. senegalensis* pest occurrences because they cohabitate with the tree in urban or agroforestry contexts (Orwa et al., 2009) but do not engage with commoditized products derived from the trees.

Based on our field observation, attack rates and production losses were higher in Tanguieta than in Toffo (Table 3). In addition, using the current wood production and the reported market price of non-damaged lumber, we found that Tanguieta and Toffo experienced losses of approximately 825.3 ± 635.2 and 681.2 ± 559.8 USD ha⁻¹, respectively, due to pest attacks. Wood loss estimation only applied to mature stands where wood-destroying insects caused severe damage. Wood production losses were higher in Tanguieta because of the greater prevalence of wood borers. In Tanguieta and Toffo, beetle pupae were isolated from the inner bark of severely attacked trees. Bark and wood-boring beetles have already been reported as economically threatening pests in natural and planted forests (Fierke et al., 2005; Schloss et al., 2006; Yousuf et al., 2014; Fettig, 2016; Rassati et al., 2016). Wood loss across two of the three study sites was significant, as was the proportion of lost lumber from insect-damaged wood. Damage from insect feeding and breeding in the phloem can destroy the inner bark (Neumann and Morey, 1984), although feeding attacks are more damaging than breeding attacks (Waterhouse and Sands, 2001). As reported by Griffiths (2001), Nair (2001; 2007), and Sokpon and Ouinsavi (2002), the engineering-quality destruction in the wood concurred with our observations. While other co-variables could be involved in the trunk deformation mechanism, it is more likely that pest attacks predispose trees to trunk deformation.

The price of damaged lumber was approximately one-seventh lower than damage-free lumber, assuming pest damage did not render the wood unsuitable for lumber processing. Our estimations confirmed the assumption that severe attacks by shoot borers can negatively impact timber value (Opuni-Frimpong et al., 2008). Significant economic damage was associated with wood-borer pests, but Griffiths (2001) previously reported substantial economic damage caused by shoot-borer problems. Shoot boring and defoliation predispose trees to trunk deformation because the causal agents operate from the top of the tree (Sokpon and Ouinsavi, 2002), leading to bifurcation (Floyd, 2001; Nair, 2001; Sokpon and Ouinsavi, 2002; 2004). Nevertheless, trees can still produce high-quality wood without wood-borer pests. While the impacts of bifurcation on wood quality are less severe than those from wood boring, they may cause severe economic losses if occurring at a low stem height. Our economic assessment depended on the current wood volume in the stand, implying that all factors (including time) that control the wood production might be a potential source of variation. Nonetheless, it provided a relative estimate of the pest-related loss in plantations of different ages at different spatial scales.

Interviewees asked for help to alleviate the production and economic losses related to pests in *K. senegalensis* plantations because they have not yet found reliable ways to control them. In more than 23 tropical countries, chemical controls for *Hypsipyla* shoot borers are used. However, no chemical or application technology provides reliable, cost-effective, and environmentally sound protection against any high-value *Meliaceae* tree species for the period required to produce a marketable stem (Wylie, 2001). The biology of the insects, the nature of their damage, the constraints imposed by the microclimate, and the mandatory period of protection needed for adequate protection are the reasons for chemical control failures. The challenge is enormous, and more efforts are required to provide plantation managers with efficient, sustainable pest control approaches (Sokpon and Ouinsavi, 2004).

CONCLUSION

We described and categorized forest pest occurrence and damage in stands of *K. senegalensis* in Benin, estimated wood loss along with the related economic impact, and discussed the biology and ecology behind the interactions between the pests and the host. We found that pest occurrence and damage severity to *K. senegalensis* varied with the age and size class structure of the plantations. Shoot borers and defoliators are destructive in a young plantation, while wood borers damage a mature plantation. These results suggest that a follow-up of the developmental stages of both pest and host before, during, and after the damage will be necessary to implement integrated pest management and reduce the tremendous amount of wood loss. Long-term studies involving seasonal observations will provide a more detailed assessment of wood destruction's behavioral mechanism in *K. senegalensis*.

Acknowledgment

We are thankful to A. Kotin, M. Agokoli, R. Gohoungbe, E. Edou, Y. Adjadja, R. Gbaguidi, M. Orou Matilo, and S. Kakpo for their facilitation and support during the data collection. Thanks to M. O'Brien for his helpful comments on the earlier versions of the manuscript.

REFERENCES

- Adams AS, Currie CR, Cardoza Y, Klepzig KD, Raffa KF (2009). Effects of symbiotic bacteria and tree chemistry on the growth and reproduction of bark beetle fungal symbionts. *Canadian Journal of Forest Research*, 39: 1133-1147.
- Adomou AC (2005). Vegetation patterns and environmental gradients in Benin: Implications for biogeography and conservation. Dissertation, Wageningen University, Netherlands.
- Akpona TJD, Idohou R, Assogbadjo A, Salako KV, Glèlè Kakaï R (2016). History, impact of soil types on stand structure and growth of the dry zone mahogany (*Khaya senegalensis* (Desr.) A.Juss.) in plantation in Benin (West Africa). *Environment and Ecology Research*, 4: 193-199.
- Bassett MA, Baumgartner JB, Hallett ML, Hassan Y, Symonds MRE (2011). Effects of humidity on the response of the bark beetle *Ips grandicollis* (Eichhoff) (Coleoptera: Curculionidae: Scolytinae) to synthetic aggregation pheromone. *Australian Journal of Entomology*, 50: 48-51.
- Bodeker G, Burford G (2005). Medicinal plant biodiversity and local healthcare: Sustainable use and livelihood development. In: Bodeker G, Burford G (ed) *Traditional, complementary, and alternative medicine: Policy and public health perspectives*. Imperial College Press, London, pp 145-166.
- Botha J, Witkowski ETF, Shackleton CM (2004). The impact of commercial harvesting on *Warburgia salutaris* ('pepper-bark tree') in Mpumalanga, South Africa. *Biodiversity and Conservation*, 13:



1675-1698.

Carson WP, Cronin JP, Long ZT (2008). A general rule for predicting when insects will have strong top-down effects on plant communities: On the relationship between insect outbreaks and host concentration. In: Weisser WW, Siemann E (ed) *Insects and ecosystem function*. Springer, Berlin, pp 193-211.

Carson WP, Root RB (2000). Herbivory and plant species coexistence: Community regulation by an outbreaking phytophagous insect. *Ecological monographs*, 70: 73-99.

Chase JM, Leibold MA, Downing AL, Shurin JB (2000). The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology*, 81: 2485-2497.

Dagnelie P (1998). *Statistique théorique et appliquée. Tome 2: Inférence statistique à une et à deux dimensions*. Université de De Boeck and Larquier, Paris.

DIVA-GIS (2018). Free geographic (GIS) data for any country in the world. Administrative areas data for Benin. www.diva-gis.org/datadown. Accessed 13 March 2018.

Djotan AKG, Aoudji AKN, Tessi DRY, Kakpo SB, Gbetoho AJ, Kourouma K, Ganglo JC (2018). Vulnerability of *Khaya senegalensis* Desr & Juss to climate change and to the invasion of *Hypsipyla robusta* Moore in Benin (West Africa). *International Journal of Biological and Chemical Sciences*, 12: 24-42.

Ennion RC (2003). Evaluation of four *Taungya* permanent big leaf mahogany plots, aged 36 to 38 years, in Belize. In: Lugo AE, Colón JCF, Alayón M (ed) *Big-leaf mahogany: genetics, ecology, and management*. Springer, New York, pp 362-374.

Erbilgin N, Nordheim E V., Aukema BH, Raffa KF (2002). Population dynamics of *Ips pini* and *Ips grandicollis* in red pine plantations in Wisconsin: Within- and between-year associations with predators, competitors, and habitat quality. *Environmental Entomology*, 31: 1043-1051.

Fettig CJ (2016). Native bark beetles and wood borers in Mediterranean forests of California. In: Paine TD, Lieutier F (ed) *Insects and diseases of Mediterranean forest systems*. Springer, Cham, pp 499-528.

Fierke MK, Kinney DL, Salisbury VB, Crook DJ, Stephen FM (2005). Development and comparison of intensive and extensive sampling methods and preliminary within-tree population estimates of red oak borer (Coleoptera: Cerambycidae) in the Ozark mountains of Arkansas. *Environmental Entomology*, 34: 184-192.

Floyd RB (2001). International workshop on *Hypsipyla* shoot borers in Meliaceae: general conclusions and research priorities. In: Floyd RB, Hauxwell C (ed) *Hypsipyla* shoot borers in Meliaceae. ACIAR, Canberra, pp 183-187.

Goussanou C., Guendehou S, Assogbadjo AE, Kaire M, Sinsin B, Cuni-Sanchez A (2016). Specific and generic stem biomass and volume models of tree species in a West African tropical semi-deciduous forest. *Silva Fennica*, 50 :1474.

Griffiths MW (2001). The biology and ecology of *Hypsipyla* shoot borers. In: Floyd RB, Hauxwell C (ed) *Hypsipyla* shoot borers in Meliaceae. ACIAR, Canberra, pp 74-80.

Hofstetter RW, Cronin JT, Klepzig KD, Moser JC, Ayres MP (2006). Antagonisms, mutualisms and commensalisms affect outbreak dynamics of the southern pine beetle. *Oecologia*, 147: 679-691.



- Horak M (2001). Current status of the taxonomy of *Hypsipyla ragonot* (Pyralidae: Phycitinae). In: Floyd RB, Hauxwell C (ed) *Hypsipyla shoot borers in Meliaceae*. ACIAR, Canberra, pp 69-73.
- Keenan RJ, Reams GA, Achard F, de Freitas J V., Grainger A, Lindquist E (2015). Dynamics of global forest area: results from the FAO global forest resources assessment 2015. *Forest Ecology and Management*, 352: 9-20.
- Lombardero MJ, Ayres MP, Hofstetter RW, Moser JC, Lepzig KD (2003). Strong indirect interactions of *Tarsonemus* mites (Acarina: Tarsonemidae) and *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Oikos*, 102: 243-252.
- Long ZT, Mohler CL, Carson WP (2003). Extending the resource concentration hypothesis to plant communities: effects of litter and herbivores. *Ecology*, 84: 652-665.
- Maloney PE, Rizzo DM (2002) Pathogens and insects in a pristine forest ecosystem: the Sierra San Pedro Martir, Baja, Mexico. *Canadian Journal of Forest Research*, 32: 448-457.
- Mathre DE (1964). Pathogenicity of *Ceratocystis ips* and *Ceratocystis minor* to *Pinus ponderosa*. *Contributions from Boyce Thompson Institute*, 22: 363-389.
- Morgan FD (1989). Forty years of *Sirex noctilio* and *Ips grandicollis* in Australia. *New Zealand Journal of Forestry Science*, 19: 198-209.
- Nair KSS (2001). Pest outbreaks in tropical forest plantations: Is there a greater risk for exotic tree species? CIFOR, Bogor.
- Nair KSS (2007). *Tropical forest insect pests: Ecology, impact, and management*. Cambridge University Press, Cambridge.
- Neuenschwander P, Sinsin B, Goergen G (2011). Protection de la nature en Afrique de l'Ouest: Une liste rouge pour le Bénin. *International Institute of Tropical Agriculture*, Ibadan.
- Neumann FG, Morey J (1984). Studies on the introduced bark beetle *Ips grandicollis* (Eichhoff) in Victorian radiata pine plantations. *Australian Forest Research*, 14: 283-300.
- Neumann FG (1987). Introduced bark beetles on exotic trees in Australia with special reference to infestations of *Ips grandicollis* in pine plantations. *Australian Forestry*, 50: 166-178.
- Newton ACC, Baker P, Ramnarine S, Mesén JFF, Leakey RRBRB (1993). The mahogany shoot borer: Prospects for control. *Forest Ecology and Management*, 57: 301-328.
- Nikiema A, Pasternak D (2008). *Khaya senegalensis* (Desr.) A. Juss. Record from PROTA4U. In: Louppe D, Oteng-Amoako AA, Brink M (ed) PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale), Wageningen, Netherlands. <http://www.prota4u.org/search.asp>. Accessed 19 December 2019.
- Opuni-Frimpong E, Karnosky DF, Storer AJ, Cobbinah JR (2008). Silvicultural systems for plantation mahogany in Africa: Influences of canopy shade on tree growth and pest damage. *Forest Ecology and Management*, 255: 328-333.
- Orwa C, Mutua A, Kindt R, Jamnadass R, Anthony S (2009). Agroforestry tree database: a tree reference and selection guide version 4.0. https://apps.worldagroforestry.org/treedb2/AFTPDFS/Khaya_senegalensis.PDF Accessed 19 December 2019.



- Paul C, Weber M (2013). Intercropping *Cedrela odorata* with shrubby crop species to reduce infestation with *Hypsipyla grandella* and improve the quality of timber. *International Scholarly Research Notices Forestry* 2013: 637410.
- Payn T, Carnus JM, Freer-Smith P, Kimberley M, Kollert W, Liu S, Orazio C, Rodriguez L, Silva LN, Wingfield MJ (2015). Changes in planted forests and future global implications. *Forest Ecology and Management*, 352: 57-67.
- Phillips C (2002). Learning to live with *Sirex* and *Ips*. *Australian Forest Grower*, 25: 19.
- Pretzsch H, Biber P, Uhl E, Dahlhausen J, Rötzer T, Caldentey J, Koike T, van Con T, Chavanne A, Seifert T, Toit B du, Farnden C, Pauleit S (2015). Crown size and growing space requirement of common tree species in urban centres, parks, and forests. *Urban Forestry and Urban Greening*, 14: 466-479.
- Preuhsler T (1981) Ertragskundliche Merkmale oberbayerischer Bergmischwald-Verjüngungsbestände auf kalkalpinen Standorten im Forstamt Kreuth. *Forstwissenschaftliches Centralblatt*, 100: 313-345.
- Rassati D, Lieutier F, Faccoli M (2016). Alien wood-boring beetles in Mediterranean regions. In: Paine TD, Lieutier F (ed) *Insects and diseases of Mediterranean forest systems*. Springer, Cham, pp 293-327.
- Millenium Ecosystem Assessment (2005). *Ecosystems and human well-being: synthesis*. Island Press, Washington.
- Schloss PD, Delalibera I, Handelsman J, Raffa KF (2006) Bacteria associated with the guts of two wood-boring beetles: *Anoplophora glabripennis* and *Saperda vestita* (Cerambycidae). *Environmental Entomology*, 35: 625-629.
- Sinsin B, Matig OE, Assogbadjo AE, Gaoué OG, Sinadouwirou T (2004). Dendrometric characteristics as indicators of pressure of *Afzelia africana* Sm. dynamic changes in trees found in different climatic zones of Benin. *Biodiversity and Conservation*, 13: 1555-1570.
- Sokpon N, Ouinsavi C (2002), Utilisations du *Khaya senegalensis* en médecine traditionnelle au Bénin. *Revue de Médecines et Pharmacopées Africaines*, 16: 9-19.
- Sokpon N, Ouinsavi C (2004). Gestion des plantations de *Khaya senegalensis* au Benin. *Bois & Forêts des Tropiques*, 279: 37-46.
- Stone C, Penman T, Turner R (2012). Managing drought-induced mortality in *Pinus radiata* plantations under climate change conditions: a local approach using digital camera data. *Forest Ecology and Management*, 265: 94-101.
- The Money Converter (2019). Convert from West African Franc (XOF) to United States Dollar (USD). In: *Forex data by Xignite*. <https://themoneyconverter.com/XOF/USD>. Accessed 5 November 2019.
- Waterhouse DF, Sands DPA (2001). *Classical biological control of arthropods in Australia*. ACIAR, Canberra.
- White F (1986). *La végétation de l'Afrique*. IRD Editions, Paris.
- Wood SL (1982). The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs*, 6: 1-1359.



Wylie FR (2001). Control of *Hypsipyla* spp. shoot borers with chemical pesticides: a review. In: Floyd R, Hauxwell C (ed) *Hypsipyla* shoot borers in Meliaceae. ACIAR, Canberra, pp 109-115.

Yousuf F, Gurr GM, Carnegie AJ, Bedding RA, Bashford R, Gitau CW (2014). Biology of the bark beetle *Ips grandicollis* Eichhoff (Coleoptera: Scolytinae) and its arthropod, nematode and microbial associates: a review of management opportunities for Australia. *Austral Entomology* 53: 298-316.

Zanetti R, Abreu CS, Silveira SHP, Andrade ED (2017). First report of *Hypsipyla grandella* (Lepidoptera: Pyralidae) on African mahogany *Khaya ivorensis*. *Scientia Agricola*, 74: 492-494.

References