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Impacts of *Chromolaena odorata* on native trees' regeneration in the Lama secondary forests in Benin, West Africa

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Photo 1.
Invasion of Lama secondary forests by *C. odorata* where a man of 1.85 m is almost hidden.
Photo A. J. Gbètoho.

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RÉSUMÉ

Impact de *Chromolaena odorata* sur la régénération d'arbres natifs dans les forêts secondaires de la Lama au Bénin, Afrique de l'ouest

Les espèces exotiques envahissantes (EEE) peuvent avoir un impact négatif sur la régénération forestière. Cette étude a pour objectif d'évaluer les impacts de *Chromolaena odorata* sur la régénération arborée dans des forêts secondaires, ainsi que les moyens de les contrôler à bas prix. Les données ont été recueillies dans 77 parcelles rectangulaires de 0,5 ha dans des forêts secondaires de la forêt classée de La Lama (Bénin, Afrique occidentale). Dans chaque parcelle, on a mesuré le dbh d'arbres (de dbh ≥ 10 cm) les rejets avec un ruban métrique, compté le nombre de rejets et mesuré la densité de recouvrement avec un densitomètre. La couverture de *C. odorata*, l'EEE ciblée, a été estimée dans une échelle de 0 (absence) à 100 % (couvert fermé). Les taillis et rejets ont été catégorisés dans trois groupes en fonction de leurs besoins de lumière (pionnier, non-pionnier léger besoin, et tolérant à l'ombre). *C. odorata*, densité de recouvrement, densité d'arbres, surface terrière, diamètre principal et recouvrement moyen ont été comptés et utilisés comme variables. Des coefficients de corrélation bilatérale entre les variables ont été calculés. Une analyse de régression, utilisant des modèles linéaires généralisés dans le logiciel R pour mettre en corrélation les variables du nombre de taillis/rejets par catégorie, a montré que *C. odorata* était en train d'éviter à la fois le développement des semis et des rejets de toutes les espèces, indépendamment de leurs catégories de besoin de lumière. Cependant, le couvert fermé avait une corrélation négative avec le couvert de l'herbe et peut être un moyen biologique de contrôler les EEE dans des forêts secondaires et dégradées.

Mots-clés : régénération naturelle, espèces exotiques envahissantes, contrôle biologique, facilitation écologique, restauration forestière, gestion forestière, Bénin, Afrique occidentale.

ABSTRACT

Impacts of *Chromolaena odorata* on native trees' regeneration in the Lama secondary forests in Benin, West Africa

Invasive Alien Species (IAS) could have negative impacts on forest regeneration. This study aimed to assess the impacts of *Chromolaena odorata* on tree regeneration in secondary forests and means of controlling it at low cost. Data were collected in 77 rectangular 0.5 ha plots in secondary forests of the Lama forest reserve (Benin, West Africa). In each plot, we measured the dbh of trees (of dbh ≥ 10 cm) and saplings with diameter tape, counted the number of seedlings and measured the canopy cover using a densiometer. The cover of *C. odorata*, the target IAS, was estimated on a scale from 0 (absence) to 100% (entire canopy). The seedlings and saplings were categorised into three light-requirement groups (pioneer, non-pioneer light-demanding, shade-tolerant). *C. odorata* and canopy cover, tree density, basal area, mean diameter and mean canopy cover were computed and used as variables. Bilateral coefficients of correlation between the variables were computed. Regression analysis, using generalized-linear models in R software to correlate the variables to the number of seedlings/saplings per category, showed that *C. odorata* was precluding the development of both seedlings and saplings of all species, whatever their light requirement category. However, canopy closure was negatively correlated with grass cover and could be a biological mean to control IAS in secondary and degraded forests.

Keywords: natural regeneration, invasive alien species, biological control, ecological facilitation, forest restoration, forest management, Benin, West Africa.

RESUMEN

Impacto de *Chromolaena odorata* en la regeneración de árboles nativos en los bosques secundarios de La Lama en Benín, África occidental

Las especies exóticas invasoras (EEI) pueden impactar negativamente en la regeneración forestal. Este estudio tiene como objetivo evaluar el impacto de *Chromolaena odorata* en la regeneración arbórea de bosques secundarios, así como los medios de controlarlo a bajo coste. Los datos se recogieron en 77 parcelas rectangulares de 0,5 ha en bosques secundarios de la Reserva Forestal de La Lama (Benín, África occidental). En cada parcela, medimos la dbh de los árboles (de dbh ≥ 10 cm) y los pimpollos con cinta métrica, contamos el número de plantíos y medimos la densidad de recubrimiento mediante un densitómetro. El dosel de *C. odorata*, el EEI objetivo, se estimó en una escala de 0 (ausencia) a 100% (recubrimiento completo). Los plantíos y pimpollos se categorizaron en tres grupos según su necesidad lumínica (pionero, no pionero con exigencia lumínica y tolerante a la sombra). Se computó el número de *C. odorata,* su densidad de recubrimiento, la densidad arbórea, el área basal, el diámetro medio y el recubrimiento medio, que se usaron como variables. Se calcularon los coeficientes bilaterales de correlación entre las variables, y se realizó un análisis de regresión, utilizando modelos lineales generalizados con el software R para correlacionar las variables con el número de plantíos/pimpollos por categoría. *C. odorata* impedía el desarrollo de ambos, plantíos y pimpollos de todas las especies independientemente de la categoría de necesidad lumínica. Sin embargo, el cierre por recubrimiento estaba negativamente correlacionado con la cubierta herbácea y podría ser un medio biológico para controlar las EEI en bosques secundarios y degradados.

Palabras clave: regeneración natural, especies exóticas invasoras, control biológico, facilitación ecológica, restauración forestal, gestión forestal, Benín, África occidental.

Introduction

The improvement of natural regeneration is the best way to support the recovery of the structure and biodiversity of tropical secondary forests (Martinez-Ramos *et al.*, 2016). Several factors affect forest regeneration during early forest succession and these include: the intensity of disturbances, the distance to seed sources, their dispersion to the degraded site, the invasion by alien species, the regeneration microsites, the predation of seeds and seedlings, climate change, etc. (Hooper *et al.*, 2005; Liira *et al.*, 2011).

Some IAS produce substances that hinder germination of native species (Hu and Zhang, 2013). Moreover, seedlings and saplings of shade tolerant and light-demanding species respond differently to the light environment induced by IAS, with a negative effect on light-demanding species (Honu and Dang, 2000). According to the ninth Aïchi's target about Biodiversity, IAS must be controlled or eradicated. However, some findings suggested that IAS may act as nursery plants to native species and facilitators of the evolution of ecosystems to stable point (MacDougall and Turkington, 2005; Didham *et al.*, 2005). Furthermore, the rarity of native species in invaded fields may be the consequence of dispersal limitation, rather than exclusion from competition (Gurevitch and Padilla, 2004).

In Lama forest, several part of the secondary forests and fallows stayed generally invaded, mainly by *Chromolaena odorata* (L.) R.M.King, an invasive alien grass, which seems to be slowing down forest regeneration according to forest managers and previous observations (Hounkpèvi *et al.*, 2011; Gbetoho *et al.*, 2016). The recruitment of secondary forests now dominated by light-demanding pioneer trees was possible where forest managers had controlled *C. odorata* through cutting. The control of *C. odorata* has been the focus of several international workshops in the past (Zachariades *et al.*, 2002). It is therefore necessary to determine whether *C. odorata* plays a facilitative role or was hindering regeneration processes in Lama forest and in the last case, to search for the best cost-effective way to control it.

Chemical control of cuttings is not achievable at a large scale without negative impact on the environment or will not be cost effective (Goodall and Erasmus, 1996). Biological control through the introduction of natural enemies as it was the case for *C. odorata* may have drastic long term consequences since these enemies are also exotic and may become invasive (Zachariades *et al.*, 2002). The suppressing effect of forest cover on the light-demanding grasses, which is a form of "amensalism", may be the best means of control of the light-demanding IAS while facilitating the establishment of the other species (Liira *et al.*, 2011).

To our knowledge, there is scarce literature on the impact of IAS on forest functioning in Benin. Moreover, any concrete actions on IAS have been elaborated to control *C. odorata* and *Hyptis suaveolens* (L.) Poit., the two main IAS that are affecting forests functioning in Benin (Aboh, 2008). The present study was aiming to assess the impact of *C. odorata* on secondary forests regeneration and the ways of a low cost control. Specifically, the study was aiming at: assessing the impact of *C. odorata* on the regeneration of Lama secondary forests; determining the impact of stand structure on *C. odorata* cover. We asked: How the abundance and diversity of light-demanding and shade-tolerant tree species vary with the cover of *C. odorata* in Lama secondary forests? How the coverage of *C. odorata* vary with stand structure in general, and canopy cover in particular? We hypothesized that the cover of *C. odorata* reduces the abundance and diversity of seedlings and saplings of light-demanding tree species and that *C. odorata* coverage is reduced by dense canopy cover.

Photo 2.
Invasion in Lama secondary forests reduced under tree canopy, so regeneration may start.
Photo A. J. Gbètoho.

Materials and Methods

Study area

The present study was done in the natural forest of Lama located in south-Benin (6°55'-7°00'N; 2°04'-2°12'E). The forest underwent severe deforestation for shifting agriculture purposes and now covers 4,785 ha with only 1,900 ha of fragments of non-degraded forests, the remaining forest is dominated by secondary forests and fallows invaded by *C. odorata*. The Lama forest is an edaphic semi-deciduous forest with its particular floristic composition dominated by *Dialium guineense* Willd. and *Diospyros mespiliformis* Hochst. ex A.DC. The secondary forests were dominated by *Lonchocarpus sericeus* (Poir.) Kunth, *Anogeissus leiocarpa* (DC.) Guill. & Perr., *Ceiba pentandra* (L.) Gaertn and *Albizia zygia* (DC.) J.F.Macbr. (Gbetoho *et al*., 2016). The study area is submitted to a subequatorial climate with a mean annual rainfall of 1,124 mm. The main rainy season extends from March to July, and the short rainy season lasts from September to November. The mean annual temperature is 27.5°C and the annual relative humidity is higher than 60%. The topography is almost flat and the vertisols, "black cotton soils", are dominant.

Data collection

Data were collected in 77 rectangular plots of 50 m x 100 m each, randomly set in the secondary forests of Lama in 2010 (figure 1) (Gbètoho *et al.*, 2016). Each plot was divided in two square subplots of 0.25 ha and the dbh of adult trees (dbh ≥ 10 cm) were measured in 2015. Two regeneration quadrats of 10 m x 10 m were set in each subplot and the following data were collected:

- Seedlings (dbh ‹ 1 cm) and saplings (1 ≤ dbh ‹ 10 cm) of tree and shrub species were identified and counted.
- The part of each quadrat covered by *C. odorata* (*C_Cod*) was evaluated in percentage.
- The density of the canopy (*C_cov*) was evaluated using a concave spherical crown densiometer model A (Brand: Forestry suppliers). While holding the densiometer in hand under the canopy, each of its 24 cells was divided in four parts and those shaded by the canopy were counted. The result was multiplied by 1.04 to convert it in percentage. The measures were taken at the centre of each quadrat, and by facing successively the four cardinal points.

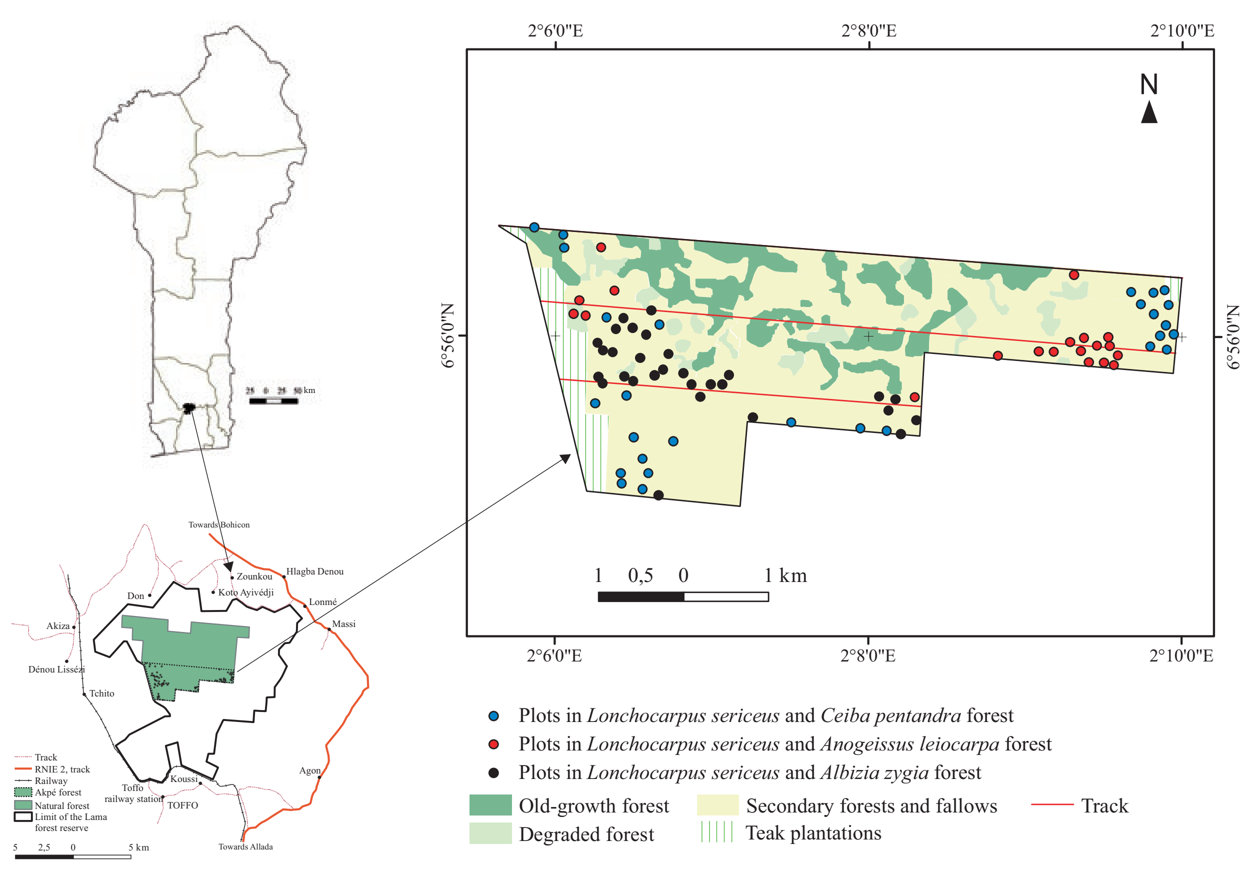

Figure 1.
Localisation of the study area and of the plots.

Data analysis

The species were categorised in three groups: pioneer species "*Pn*", non-pioneer light-demanding species "*NPLD*" and shade-tolerant "*S*'" (Hawthorne, 1995). The number of seedlings, respectively saplings, counted in the two quadrats of each sub-plot were summed up and used as response variables. The number of species in the two quadrats was also counted and used as a response variable. *C. odorata* cover (*C_Cod*) and the density of canopy (*Ccov*) were averaged at the subplot level and used as factors. The other factors include the number of adult trees (*n*), the basal area (*BA*) and the mean diameter (*Dg*) computed at the subplot level.

We assessed the correlation between the density of regeneration of each group (*Pn*, *NPLD*, *ST*) and the factors on a one hand and between the factors on a second hand, using a bilateral Pearson's coefficient of correlation. Then, Generalized Linear Models (*GLM*) were also used to check the variation of the regeneration density according to the targeted factors. In R software, the factors were selected by stepwise regression, using the Maximum Likelihood method (Olsson, 2002). The model with the lowest Bayesian Information Criterion *(BIC)* and which respected the following conditions was retained: significance of the deviance explained, normality, homogeneity and independence of the residuals (Vayreda *et al.*, 2013). The significance of the deviance was measured by a chi-square test on the deviance table. After the visualization of the residual's graphs, the normality, the homogeneity and the independence of the residuals were assessed respectively by a Shapiro-Wilk test, a Breusch-Pagan test, and a Durbin-Waston test. When the residuals were not homogenous and normally distributed, the variables were log or squareroot transformed (Vayreda *et al.*, 2013), or the distance of Mahalanobis was computed to detect and remove the aberrant individuals and this lead to the variation of the degree of freedom. The degree of freedom varied also according to the number of factors kept in the model and also because we excluded plots with responses (regeneration density) equal to 0. The selection of the models on the basis of their *BIC* allowed us to get the simplest model as possible, i.e. model with few variables, and therefore to assess only the targeted factors that highly influenced the density of regeneration.

Results

The regeneration of *A. leiocarpa* was found only in 5-25% of the plots; those of *C. pentandra* in 30 to 60% of the plots, while the regeneration of *L. sericeus*, *A. zygia*, *D. mespiliformis* and *D. guineense* were found in more than 60% of the plots.

Impact of *C. odorata* cover on the number of species in the regeneration layer

C. odorata cover (*C_Cod*) and the number of trees (*N*) had negative correlation with the number of species in the regeneration layer (respectively $r = -0.694$, $p < 0.001$; $r = -0.237$, $p < 0.05$), while canopy cover (*C_cov*) and the mean diameter *(Dg)* had a strong positive correlation with the number of species (respectively $r = 0.529$, $p < 0.001$; $r = 0.306$, $p < 0.01$). The results of the *GLM* also showed that *C_Cod* had a strong negative correlation with the number of species in the regeneration layer, and particularly with the number of *NPLD* and *ST* (table I). However, *C_Cod* was not correlated with the number of pioneer species, which was positively correlated with the number of adult trees in the plot. The deviances explained were low (R-sq < 50%) but significant ($p < 0.05$).

Impact of *C. odorata* cover on the density of seedlings/saplings

C. odorata cover (*C_Cod*) was strongly and negatively correlated with the densities of regeneration of the species while the density of the canopy (*C_cov*) was strongly and positively correlated with the same regeneration densities whatever the light requirement category (table II). The mean diameter was positively correlated with the density of regeneration of non-pioneer light-demanding (*NPLD*) and shade-tolerant (*ST*) species. The number of trees (*N*) was negatively correlated with the density of regeneration of *NPLD* while the basal area (*BA*) was positively correlated with the density of regeneration of *NPLD* (table II).

The intercepts of the models obtained after the *GLM* were positive and highly significant. *C_Cod* was highly negatively correlated to the number of seedlings and saplings

Table I.
Impact of *Chromolaena odorata* and stand structure on the number of species and specifically for pioneer (*Pn*), non-pioneer light demanding *(NPLD)* and shade-tolerant species *(ST)*. *C_Cod* = cover of *C. odorata*; *N* = number of adult trees; Df = degree of freedom; *BIC* = Bayesian information criterion.

Parameters	**All species**	***Pn* species**	***NPLD* species**	***ST* species**
Intercept	10.63***	1.40***	3.85***	4.26***
C_Cod	-0.05***	-	-0.03***	-0.02***
N	-	0.014*	-	-
Deviance explained	34%***	5%**	32%***	23%***
Df	131	131	131	131
BIC	552.9	440.75	393.31	407.6

***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns ≥ 0.05.

Table II.
Correlation between density of regeneration, *Chromolaena odorata* cover and dendrometric parameters.
Nr_Pn = regeneration density of pioneer species; Nr_NPLD = regeneration density of non pioneer light demanding species; Nr_ST = regeneration density of Shade-tolerant species; *C_Cod* = cover of *C. odorata*; *C_cov* = canopy cover; *N* = number of adult trees; *BA* = basal area of adult trees.

	C_Cod	***C_cov***	***N***	**Dg**	***BA***
Nr_Pn	-0.302**	0.254**	0.175	0.002	0.182
Nr_NPLD	-0.593***	0.481***	-0.231*	0.448***	0.219*
Nr_ST	-0.547***	0.400***	-0.175	0.208*	0.018
C_Cod	1	-0.803***	0.17	-0.472***	-0.295*
C_cov		1	-0.197*	0.407***	0.191*
N			1	-0.513***	0.520***
Dg				1	0.449***
BA					1

***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns ≥ 0.05.

Table III.
Models of seedlings abundance for pioneer species. *Pn* = pioneer species; Pntot = number of seedlings and saplings of pioneer species; LS = *L. sericeus*; *C_Cod* = cover of *C. odorata*; *N* = number of adult trees; *BA* = basal area of adult trees; ":" means interaction between factors; Df = degree of freedom; *BIC* = Bayesian Information Criterion.

Parameters	**Pntot**	***Pn* seedlings**	***Pn* saplings**	**LS saplings**
Intercept	16.46**	0.99	2.89***	2.77***
C_Cod	-0.06***	-0.05***	-0.03***	-0.02***
N	-0.12	0.10***	-	-
BA	-4.12*	-	-	-
N:*BA*	0.07**	-	-	-
Deviance explained	35%**	32%***	24%***	20%**
Df	93	90	104	32
BIC	538.3	468.82	361.21	106.44

***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns ≥ 0.05.

whatever of the light-requirement category considered (table III to V). The number of trees (*N*) was positively correlated to the number of seedlings of pioneer species (*Pn*) (table III), but negatively correlated to the number of saplings of *NPLD* (table IV) and the global regeneration density of *ST* (table V). *BA* was negatively correlated to the density of regeneration of *Pn* (table III) and to the number of saplings of *NPLD* (table IV). The interaction between *BA* and *N* had positive impact on the density of regeneration of *Pn* (table III) and the number of saplings of *NPLD* (table IV). The factors, only *C_Cod* in five models, explained about 21 to 41% of the variation of the number of seedlings, saplings and global regeneration of the species.

The saplings of *L. sericeus*, *H. floribunda*, *D. guineense* and *D. mespiliformis* were strongly affected by *C_Cod* (table III to V). The regressions were not conclusive for the other dominant species, such as *A. leiocarpa*, *C. pentandra*, *A. africana* and *A. zygia*. *C_Cod* explained between 17% and 41% of the variation of the number of saplings of the dominant species in the forest. In addition to the conditions stated in the section Methods, the degree of freedom varied greatly because, during the analyses, we excluded records where the targeted species were absent to avoid responses data equal to 0.

Table IV.
Models of saplings abundance for non-pioneer light demanding species. *NPLD* = non pioneer Light-Demanding; NPLDtot = number of seedlings and saplings of non pioneer light-demanding species; HO = *H. floribunda*; *C_Cod* = cover of *C. odorata*; N = number of adult trees; *BA* = basal area of adult trees; Df = degree of freedom; *BIC* = Bayesian information criterion; ":" means interaction between factors.

Parameters	**NPLDtot**	***NPLD* seedlings**	***NPLD* saplings**	**HO sap**
Intercept	16.99***	11.23***	9.60***	5.20***
C_Cod	-0.15***	-0.09***	-0.35***	-0.05***
N	-	-	-0.08*	-
BA	-	-	-1.56*	-
N:*BA*	-	-	0.02*	-
Deviance explained	35%***	29%***	31%*	32%
Df	90	108	98	61
BIC	720.4	608.88	384.33	291.74

***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns ≥ 0.05.

Table V.
Models of saplings abundance for shade-tolerant species. *ST* = shade-tolerant species; STtot = number of seedlings and saplings of *ST* species; *C_Cod* = cover of invasive alien species; *Ccov* = canopy cover; *BA* = basal area of adult trees; *N* = number of adult trees.

Parameters	**STtot**	***ST*seedlings**	***ST*saplings**	***Diospyros mespiliformis***	***Dialium guineense***
Intercept	31.88***	21.32***	6.02***	2.97***	2.70***
IAS	-0.17***	-0.16***	-0.06***	-0.03***	-0.02*
N	-0.11*	-	-	-	-
Deviance explained	33%*	23%***	41%***	37%***	17%
Df	96	98	101	38	31
BIC	686.82	688.21	450.14	130.75	121.92

***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns ≥ 0.05.

Correlations between dendrometric parameters and the cover of *C. odorata*

The bilateral coefficients of correlation (table II) showed the relation between the factors. *C_cov*, *Dg* and *BA* were positively correlated, but were all negatively correlated to *C_Cod*. The number of trees, *N*, was negatively correlated both to *C_cov* and *Dg*, but positively correlated to *BA*.

Discussion and conclusion

The vertisols of Lama forest make the site be selective of species. The dominant species of the Lama forests are well adapted to the site and form gregarious stands even in old-growth forests and in the secondary forests. In tropical ecosystems, seed dispersion is enhanced by wind for light seeds, or by animals (birds, bats, monkeys, rodents, etc.) for heavy seeds. Regeneration of *L. sericeus*, *D. guineense* and *D. mespiliformis*, which are barochorous species, were more common than the regeneration of *A. leiocarpa* and *C. pentandra*, which are wind dispersal species. Species dispersed by animals have more success for regeneration in degraded fields than wind-dispersed species (Montoya *et al.*, 2008). However, dispersion by animals is generally successful when remnant trees or shrubs exist in fallows of degraded fields (Chapman *et al.*, 2008). Therefore, at the level of a forest block, when dispersion is not a limiting factor, the establishment of seedlings and saplings of canopy species growing in forest patches is mainly affected by post-dispersal events. Our regeneration plots were set near tree patches where seed-trees of the dominant pioneer tree were present and their seeds were disseminated through invaded site.

Photo 3.
Invasion of Lama secondary forests by *C. odorata*, showing a man of 1.85 m almost hidden.
Photo A. J. Gbètoho.

Photo 4.
Under *C. odorata* cover, the stacking of its dead and living biomass created darkness enlightened by the flash of our camera and humidity; a seedling of a shade-tolerant species was emerging.
Photo A. J. Gbètoho.

Photo 5.
Under *C. odorata* cover, the stacking of its dead and living biomass created darkness enlightened by the flash of our camera and humidity; no seedling was found.
Photo A. J. Gbètoho.

C. odorata impeded the regeneration of all species

Openings in the canopy allow the development of a large number of light-demanding species and the closure of the canopy favours the establishment of shade-tolerant species because shade-tolerant may stagnate for long time under shade (Baraloto, 2003; Decocq *et al.*, 2004). Abundance of grass cover in the understorey may have the same effect on light-demanding species compared to shade-tolerant species (photos 1 and 4). Species richness in the regeneration layer, seedlings and saplings abundance, whatever their light requirement category, decreased with the cover of *C. odorata*. Regeneration occurred under the cover of *C. odorata* as already stated by Ganglo (2005). However, there were more species on the one hand, and more seedlings and saplings of the species on the other hand, in areas not invaded compared to areas invaded (photo 3 vs photo 6). Light-demanding seedlings had low growth and high mortality at seedlings stage under the cover of *C. odorata* and could grow up only after the removal of that grass (Honu and Dang, 2000). The rarity of shade-tolerant species under high *C. odorata* cover (photos 4 and 5) may be explained by several factors and need more investigations.

IAS are considered as nursery plants or passengers for the stability of open savannah, because in such ecosystems, IAS maintain the open structure by precluding the establishment of trees/shrubs while holding shade-tolerant grasses and forbs (McDougall and Turkington, 2005). However forests architecture is determined by trees and conditions that impede the installation of trees and shrubs are barriers to, or delayer of forest recovery. The establishment of seedlings and saplings is also determined by the existence of suitable regeneration microsites (soil conditions, site productivity, etc.) (Liira *et al.*, 2011), but due to our current objectives, abiotic factors were not considered. The abundance of *C. odorata* was not the only factor that may be affecting forest regeneration, but explain about 20 to 40% of the variation of seedlings and saplings abundance. This high influence should be analysed together with other factors.

Improving forest cover as a possibility to reduce the cover of *C. odorata*

Several studies were conclusive after the mowing and cutting of the invasive grass (Honu and Dang, 2000; MacDougall and Turkington, 2005), which is not the case in natural conditions in absence of other disturbances. The present study considered the variation of the density of regeneration under different coverage of *C. odorata*. Attempts to rear natural enemies, of which *Pareuchaetes pseudoinsulata* Rego Barros (Lepidoptera) to reduce *C. odorata* cover (Zachariades *et al.*, 2002) was conclusive but may have other impact on the environment.

The cover of *C. odorata* decreased with canopy cover, mean diameter and basal area. These parameters are expression of the canopy closure. Canopy closure exerts a suppressing effect on herb layer including seedlings and saplings of pioneer trees, which is termed amensalism (Page and Cameron, 2006; Liira *et al.*, 2011). The interaction between tree density and basal area represents the standing biomass and consequently an amount of shade provided which may reduce *C. odorata*'s coverage and may increase regeneration. Therefore, trees and shrubs could be facilitators to seedlings and saplings in invaded areas by reducing herb cover and supporting seed-dispersers (Castro *et al.*, 2004; Gomez-Aparicio *et al.*, 2004). However, the present study did not reveal whether pioneer species raised out to reduce *C. odorata* cover, or raised out after the diminution of *C. odorata* cover (photos 1, 2, 6). The negative influence of tree density and basal area on the richness or abundance of pioneer trees' regeneration is justified by the incapacity of pioneer to regenerate under shade (Bonino and Araujo, 2005). The same applied to the relation between canopy cover and the number of trees, and between mean diameter and the number oftrees, and was already reported by Gbetoho *et al.* (2016) in the Lama forest.

The negative influence of tree density on ST abundance could be viewed in terms of the age of the forest. Indeed, in the secondary forests of Lama, tree density decreased with the age of the forests (Gbetoho *et al.*, 2016), while the abundance of seedlings and saplings of shade-tolerant trees increase with the age of the stands. Therefore, the recruitment of ST increase with the age of the forest.

Photo 6.
Canopy cover mainly composed by *L. sericeus* trees which have produced shade in the understorey; *C. odorata* was absent and species richness was high.
Photo A. J. Gbètoho.

The relation between canopy cover and dbh were stronger than the relation between canopy cover and basal area. Therefore, large trees that support dense canopy are more able to reduce the cover of *C. odorata*. Actions should enhance recovery of light-demanding species in gaps while enhancing regeneration of shade-tolerant species in the understorey of the secondary forests. More investigation is needed to understand the complex interactions between several abiotic and biotic factors.

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