Available online at www.sciencedirect.com

SCIENCE DIRECT®

Forest Ecology and Management 215 (2005) 329–338

Forest Ecology and Management

www.elsevier.com/locate/foreco

Does forest gap size affects population size, plant size, reproductive success and pollinator visitation in *Lantana camara*, a tropical invasive shrub?

Ørjan Totland [a,*], Philip Nyeko [b], Anne-Line Bjerknes [a],
Stein Joar Hegland [a], Anders Nielsen [a]

[a] *Department of Ecology and Natural Resource Management, The Norwegian University of Life Sciences,*
P. O. Box 5003, N-1432 Ås, Norway
[b] *Department of Forest Biology and Ecosystems Management, Makerere University, P.O Box 7062, Kampala, Uganda*

Received 29 November 2004; received in revised form 28 April 2005; accepted 10 May 2005

Abstract

Invasive species are regarded as one of the largest global threats to biodiversity, but little is still known about the invasion of exotic plants into tropical forests. In this paper, we examine how the size and canopy openness of human-created gaps inside the Mabira forest-reserve in Uganda, affect the invasion of one of the world's most noxious weeds, *Lantana camara* L. Sub-population size inside gaps was positively related to gap size, and components of individual plant size increased with increasing gap size and canopy openness. Moreover, the reproductive effort of *L. camara* increased with gap size and canopy openness, whereas the fruit production of individual plants was unrelated to gap size and canopy openness. Finally, there was no relationship between gap size and pollinator visitation to inflorescence, but a marginally significant relationship occurred between canopy openness and pollinator visitation. Overall, our results suggest that the size of human-created gaps inside Mabira forest-reserve positively affect aspects of the population dynamics of *L. camara*. We propose strategies for a campaign aimed at removing *L. camara* from this forest-reserve, with minimal disturbance to intact forest habitats.

Keywords: Exotic; Forest gaps; Invasive species; *Lantana camara*; Management; Pollination; Tropical forests

1. Introduction

Several ecosystems around the world are invaded by various exotic plant species (Usher et al., 1988; Lonsdale, 1999). In some cases, these exotics form very dense populations that affect the population dynamics and persistence probability of native species, which may reduce the local diversity of native species (e.g. Williamson, 1996; Wilcove et al., 1998; Mack et al., 2000). Several factors may explain this phenomenon (see, e.g. Keane and Crawley, 2002; Williams et al., 1995). In most cases, the native species outperformed the alien under conditions of reduced

---

[*] Corresponding author. Tel.: +47 64965781; fax: +47 64965801.
E-mail address: orjan.totland@umb.no (Ø. Totland).

0378-1127/$ – see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2005.05.023

light, nutrient or water availability (Daehler, 2003). Thus, any change in such conditions may alter competitive relationships between exotic and native species.

Despite the large documented threats from invasive species to native biodiversity in several ecosystems (e.g. Vitousek et al., 1997; Mooney, 1999), invasive species have rarely been considered as a significant threat to the diversity of tropical forests (Fine, 2002), and while invasions have been the subject of intensive ecological research during the last two decades, this research has largely ignored tropical forests (e.g. Drake et al., 1989; Williamson, 1996; but see Fine, 2002). One reason for this neglect of tropical forests is the perception that their high species diversity makes them naturally resistant to invasion (e.g. Holdgate, 1986). However, recent studies show that the diversity of exotic species is often positively correlated with native plant species diversity (e.g. Lonsdale, 1999; Stohlgren et al., 1999), which contradicts this perception and suggests that high native species diversity by no means functions as a barrier to exotic invasion. In addition, anthropogenic disturbance that create openings in tropical forest habitats makes them susceptible to invasion by exotic species. For example, in tropical forest-reserves, trails are kept open by removing bordering vegetation to allow eco-tourists and others to experience tropical forest habitats in a convenient way, resulting in the formation of gaps of contrasting sizes along such trails. Exotic populations establishing in these gaps may serve as starting points from where seeds may disperse into pristine forest interiors or naturally disturbed patches within the forest (Murcia, 1995; Cadenasso and Pickett, 2001; but see Makana and Thomas, 2004).

We studied *Lantana camara* L. (Verbanaceae), a shrub or climbing tree native to tropical and sub-tropical south-America. *L. camara* is currently considered as one of the 10 most noxious weeds in the world (Sharma et al., 1988; Fensham et al., 1994; Anon., 2000) because of its great ability to escape cultivation and the negative effects it has on local species richness and for grazing animals when it invades natural or semi-natural habitats (e.g. Mauchamp et al., 1998; Islam et al., 2001). *L. camara* has been introduced as an ornamental plant in several parts of the tropical and sub-tropical world. Most of the attention to this species is directed towards its invasion of open habitats, such as savannas and steppes. However, it also establishes in gaps inside tropical forests, and may thereby potentially alter plant community composition in forested habitats as well (Islam et al., 2001). Although *L. camara* may potentially have a devastating impact on the community structure and dynamic on forest ecosystems throughout the tropical world, there are very few studies that focus on how basic population dynamic-related characters of this species are actually affected by artificially created gaps inside tropical forests. In this study, we examined how plant density, aspects of plant size, flower production, fruit production and pollinator attraction in *L. camara* is related to physical gap size and to canopy openness above forest gaps along tourist trails in the Mabira forest-reserve in tropical Uganda. In particular, we wanted to determine if: (1) gap size is related to the openness of the canopy above gaps, and thus the amount of light reaching the ground, (2) there is any relationship between the population size of *L. camara* and gap size and canopy openness, (3) plant size and thicket density (branch density, leaf density and leaf size) is related to gap size and canopy openness, (4) aspects of reproductive success (number of flowers, inflorescences, fruits and infructescences) is related to gap size and canopy openness and (5) pollinator visitation rate to *L. camara* inflorescences is dependent on gap size and canopy openness. An important goal of our study is to propose scientifically sound management strategies designed to counteract the invasion of tropical forest ecosystems by *L. camara*.

2. Materials and methods

2.1. Study species

Morphological descriptions of *L. camara* have been widely published (e.g. Anon., 2005). *L. camara* requires cross-pollination to set fruit (Barrows, 1976; Goulson and Derwent, 2004), and it spreads primarily through the production of seeds that are dispersed by birds (Anon., 2000). In our study site, situated at the equator, flowering and fruiting occur throughout the year. Invading *L. camara* individuals at this site may form dense thickets that can cover large areas and reach heights of up to ca. 5 m (personal observation). It may also climb up, and overtop, other species, reaching heights of up to 12 m (personal observation). Very few other species are able to grow inside the dense thickets, partly because of the great reduction of light availability, and possibly due to its proposed allelopathic properties (Gentle and Duggin, 1997; Ambika et al., 2003).

2.2. Study area

We studied *L. camara* in the Mabira forest-reserve, Mukono district, Uganda. The forest is situated ca. 20 km west of Jinja, along the Kampala-Jinja road. Mabira is a medium altitude (ca. 1000 m elevation) moist semi-deciduous secondary forest (Hamilton, 1984). The forest-reserve is ca. 306 km^2. Tourists visit Mabira forest to some extent. Because of this, the forest managers keep the trails that dissect the forest floor open, creating canopy gaps of variable size and canopy closure. The trails themselves are ca. 1–2 m wide, but gaps are often wider. *Lantana camara* is used in advertisement of Mabira forest as a species that attracts "... clouds of butterflies" (http://traveluganda.co.ug/utp/mabira.html). *L. camara* establishes in most of the gaps along the trails (personal observation). We studied gaps along the Butterfly-viewing trail that starts from the visitor centre of Mabira forest-reserve and penetrates into the forest in a ca. 4 km long loop. We also included gaps along the trail that connects the Butterfly-viewing trail with the Najjembe village.

2.3. Field methods

We conducted our field studies during late-April to early-May, 2004, within the first annual rain-season of the area, which normally lasts from March to May (the second rain season is from September to December). During March to May, the average monthly precipitation is ca. 150 mm (in Kampala).

We sampled reproductive and plant size related data of *L. camara* in 30 forest gaps along trails of the Mabira forest-reserve. We observed every patch of *L. camara* along the trail, and selected patches with branches that could be measured by a worker standing on the ground. Thus, our sample of *L. camara* plants does not include climbing plants with trunks that elevated the lowest part of foliage above ca. 2 m (ca. 20% of plants along the trail were excluded based on this criteria). We defined a gap as an open space surrounded by vegetation higher than ca. 4 m. We obtained the gap size by measuring the longest distance across the gap, and the perpendicular distance to the longest distance. We used a Canon PowerShot S1 LS digital camera to make photographs of the canopy foliage immediately above the centre of each gap and also above the largest *L. camara* patch (as judged by eyesight) in each gap. Percentage canopy openness was estimated with the computer program ImageTool 3.0. Canopy openness above patches and gap centres were highly positively correlated (Pearson $r = 0.82$, $P < 0.00001$), and for simplicity we calculated a mean canopy openness for each gap from these two measurements, and used these means in all analyses. On average, the gaps included in our study were 38.3 m^2 (95% CI = 27.5–49.2), and had a mean canopy openness of 43.4% (CI = 35.8–91.0). There was a highly significant positive relationship between gap area and canopy openness (Fig. 1, linear regression coefficient = 0.47, $P = 0.00005$, $R^2 = 0.46$).

2.3.1. Growth and reproduction

The growth architecture of *L. camara* plants makes it difficult to delimit individual plants. Therefore, we counted the number of *L. camara* patches within each gap. We defined a patch as a distinct branching system

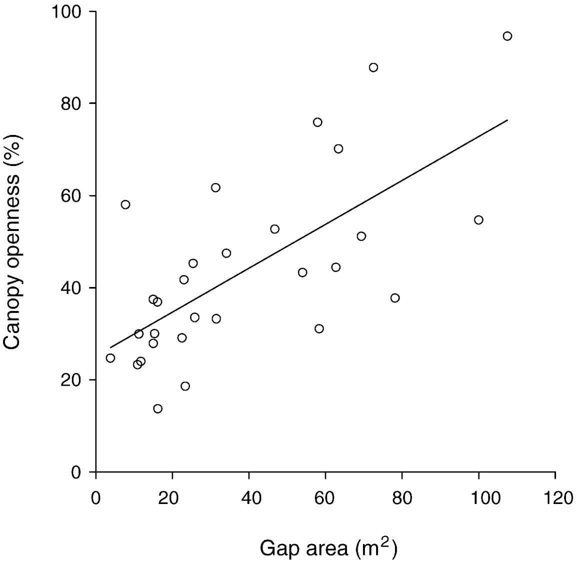


Fig. 1. Relationship between canopy gap area and canopy opening in Mabira forest-reserve, Uganda. Line shown is linear regression line.

that was clearly separated above ground from other such branching systems. Such patches may or may not be separate individuals.

We selected the largest *L. camara* patch in each gap and obtained its size by measuring the longest distance across the patch and the perpendicular width. We randomly selected five branch-tips on each patch. On the terminal 30 cm of these branch-tips, we counted the number of leaves larger than 2 cm in length and the number of lateral branches. We used the 30 cm terminal branch tip for two reasons: first, *Lantana* forms dense thickets, and working on the branch tips made fieldwork easier. Second, most leaves, and flower and fruit clusters occurred within the terminal 30 cm of branches. We also measured the density of main branches on each patch by counting the number of branches that touched a 1.5 m long rope that was randomly positioned on five separate parts on the patch.

On the same branch-tips as above, we counted the number of inflorescences, and also the number of flowers and flower buds in these inflorescences. We separated flower counts into open flowers and flower buds that had attained a purple colour (as opposed to very young green buds). In addition, we counted the number of infructescences and the total number of fruits (both ripe (black) and unripe (green)) on the same branch-tips.

2.3.2. Flower visitation by pollinators

To obtain reliable data on pollinator visitation to *L. camara* inflorescences we selected the six largest gaps included in our sample (gap size range: 46.8–78.2 m^2). In addition, we randomly selected six gaps among the remaining nineteen relatively small gaps (gap size range: 2.9–25.8 m^2). We measured pollinator visitation rates to inflorescences between 09:00 and 16:00 h, during 28 April–1 May, 2004. Measurements were conducted such that all 12 gaps were measured within all sampling days, and we rotated sampling order among gaps such that daily variation in visitation rates should not affect our assessment of inter-gap differences. We counted the number of visits to each of five randomly selected inflorescences on the largest patch within each gap during 10 min observation periods, and obtained a total of 10 such periods for each gap. We defined a visit to have occurred when we observed an insect to forage for food (nectar and/or pollen). We categorised each visitor into broadly defined taxonomic levels: Lepidoptera, Hymenoptera, Diptera and Coleoptera. After each observation period, we counted the number of red and yellow flowers in each of the five observed inflorescences, and also the number of *L. camara* inflorescences within the entire gap.

2.4. Data-analysis

We used simple linear regression (in SYSTAT, Version 10) to examine if there was any relationship between gap size or canopy openness (predictors) and the *L. camara* population size, plant size, and reproductive response parameters we obtained. The samples ($N = 29$) in these regressions consisted of data obtained for each of the gaps.

We calculated a mean visitation rate from the 10 observation periods within each of the 12 gaps that we used to measure pollinator visitation. These means were used in a linear regression to assess if pollinator visitation to *L. camara* inflorescences was related to gap size and canopy openness.

No transformations were necessary to fulfil the requirements of regression analyses.

3. Results

3.1. Population size

There was a mean of 2.2 *L. camara* patches within each gap (CI = 1.6–2.7). The number of patches within gaps was significantly (Table 1) and positively related to gap size (Fig. 2A) and canopy openness (Fig. 2B). Gap size and canopy openness explained 46 and 25% (R^2) of the variation in the number of *L. camara* patches per gap, respectively.

3.2. Plant size

On average, the largest *L. camara* patch size (length × width; our estimate of plant size) within the gaps we examined was 11.9 m^2 (CI = 8.0–15.8). Patch size was significantly positively (Table 1) related to gap size (Fig. 2C) and canopy openness (Fig. 2D). Gap size and canopy openness explained 54 and 26% of the variation in patch size, respectively.

On average, 4.02 main branches per patch (CI = 3.6–4.5) touched the 1.5 m long rope (our estimate of main

Table 1
Simple linear regression coefficients (significance values are given in parentheses) on the relationships between gap size and canopy openness (predictors) and population size, plant size and reproduction related responses of *Lantana camara* at Mabira forest-reserve, Uganda, in 2004

Responses	Gap size	Canopy openness
Population size		
Number of patches	0.68 (0.00005)	0.50 (0.005)
Plant size		
Patch area	0.73 (0.00001)	0.51 (0.005)
Density of main branches	0.34 (0.07)	0.20 (0.30)
Number of side-branches	0.17 (0.36)	0.03 (0.89)
Number of leaves per side-branch	0.001 (0.99)	0.18 (0.34)
Flower production		
Number of inflorescences per main branch	0.53 (0.004)	0.49 (0.007)
Number of flower + buds per inflorescence	0.14 (0.46)	0.15 (0.43)
Fruit production		
Number of infructescences per main branch	−0.21 (0.27)	−0.19 (0.33)
Number of fruits per infructescence	−0.25 (0.18)	−0.19 (0.32)

branch density per patch). The density of main branches was nearly significantly (Table 1) and positively related to gap size (Fig. 2E), but showed no relationship with canopy openness (Table 1, Fig. 2F). Gap size explained 11% of the variation in the density of main branches.

On the 30 cm terminal tip of a main branch, there was a mean of 18 leaves (CI = 16.6–19.4), and a mean of 2.3 side-branches (CI = 2.0–2.5). Neither the number of leaves nor the number of side branches per 30 cm terminal branch tip was related to gap area or canopy openness (Table 1).

3.3. Flower production

There was a mean of 1.4 inflorescences per 30 cm terminal tip of main branches (CI = 1.0–1.8). The number of inflorescences was significantly (Table 1) and positively related to gap size (Fig. 2G) and canopy openness (Fig. 2H). Gap size and canopy openness explained 27 and 24% of the variation in the number of inflorescences per 30 cm terminal tip of main branches.

On average, an inflorescence had a total of 10.6 flowers and/or buds (CI = 8.0–13.2). There was no relationship between the number of flowers and buds per inflorescence and gap size or canopy openness (Table 1).

3.4. Fruit production

The mean number of infructescences per 30 cm terminal tips of main branches was 0.7 (CI = 0.3–1.0), whereas the mean number of fruits per infructescence was 1.7 (CI = 0.8–2.5). Gap size and canopy openness had no direct influence on the number of infructescences per main branch tip or the number of fruit per infructescence (Table 1).

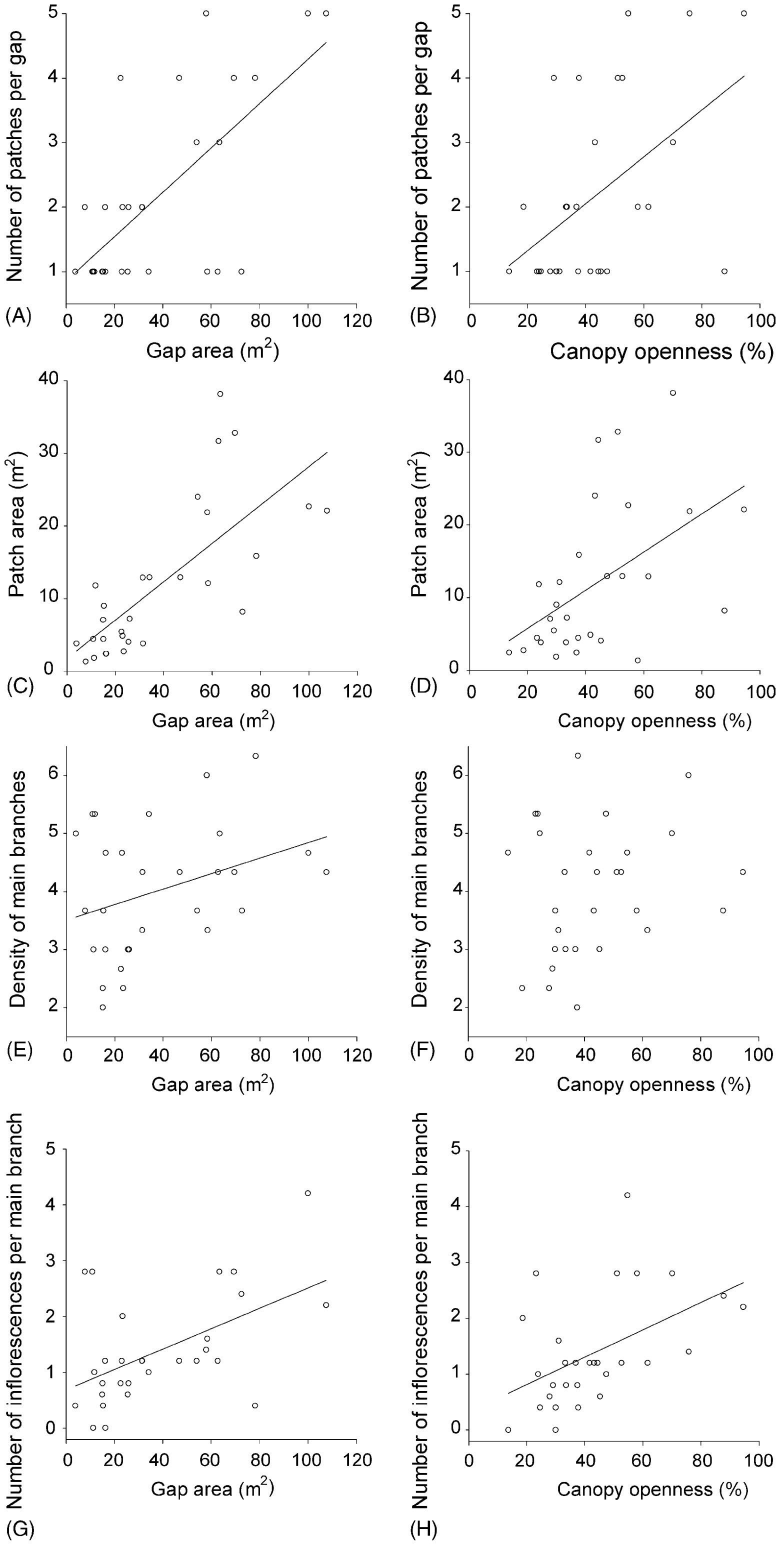
3.5. Pollinator visitation

The most frequent insect orders visiting *L. camara* inflorescence were Lepidoptera, Hymenoptera and Diptera. The mean number of visits per inflorescence per gap during 10 min was 1.7 (CI = 0.9–2.7). Linear regression showed a marginally significant positive (Fig. 3A) relationship between average pollinator visitation rate per gap and canopy openness (linear regression coefficient = 0.54, $P = 0.07$, $R^2 = 0.29$), whereas visitation rate had no relationship with gap area (Fig. 3B, $P = 0.53$).

4. Discussion

4.1. The ecology of Lantana camara in tropical forest gaps

We found significant relationships between important population dynamic parameters of *L. camara* and gap size and canopy openness inside the Mabira forest-reserve in Uganda. Not surprisingly, large gaps contained more *L. camara* patches than smaller gaps.


Number of patches per gap
Gap area (m²)
(A)
Number of patches per gap
Canopy openness (%)
(B)
Patch area (m²)
Gap area (m²)
(C)
Patch area (m²)
Canopy openness (%)
(D)
Density of main branches
Gap area (m²)
(E)
Density of main branches
Canopy openness (%)
(F)
Number of inflorescences per main branch
Gap area (m²)
(G)
Number of inflorescences per main branch
Canopy openness (%)
(H)

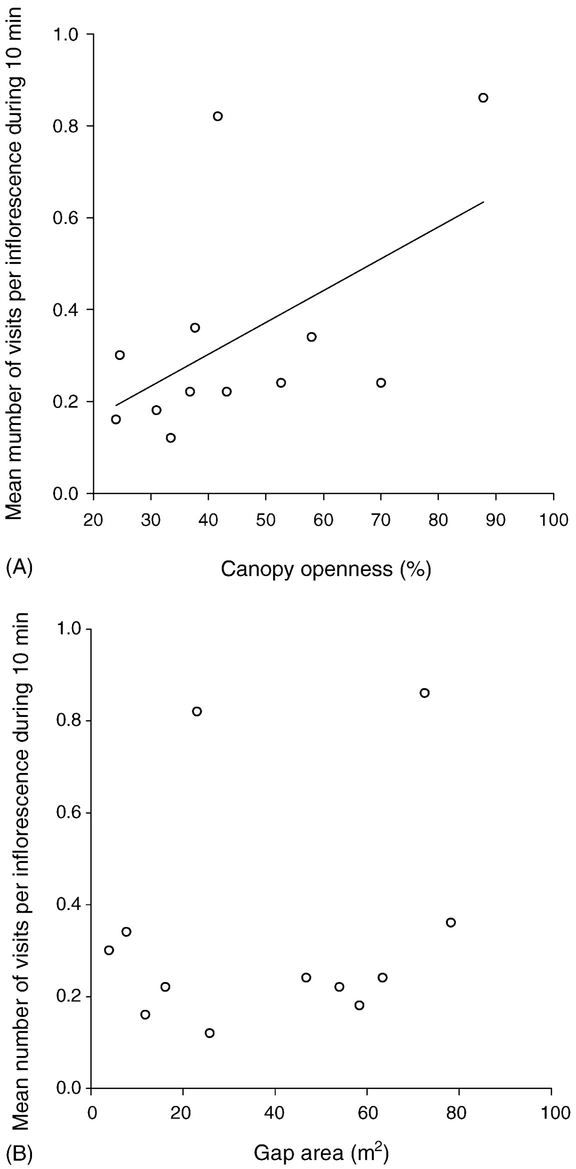


Fig. 3. Relationship between canopy openness (A) and gap area (B) and pollinator visitation rate to inflorescences of *Lantana camara* in Mabira forest-reserve, Uganda. Line shown in A is a linear regression line ($P = 0.07$).

This finding has important implications for the population ecology of *L. camara*. It means that gap size likely influences the long-term persistence of *L. camara* sub-populations in this meta-population system. Larger sub-populations within the larger gaps are likely to ensure the longer-term persistence of *L. camara* sub-populations within this forest-reserve. The higher number of patches inside larger gaps suggests that such gaps are profitable for *L. camara*. In particular, we believe that seed germination and seedling establishment success is greater in larger than in smaller gaps due to the higher light availability within the larger gaps. This has been shown for *L. camara* in Australia (Duggin and Gentle, 1998), and appears to be common in tropical forest species (Swaine and Withmore, 1988). Moreover, we also believe that the higher light availability in larger gaps (Horn, 1971; Baldocci and Collineau, 1994; Clark et al., 1996) enhance the growth of *L. camara* there (see below).

In addition to the positive relationship between gap size and number of patches, there was a positive relationship between the size of patches and gap size and canopy openness, suggesting that the higher light availability in relatively large gaps enhance the growth of individual *L. camara* shrubs, as was also suggested by results of Chandrasekaran and Swamy (2002) on *L. camara* in India. These authors found that the net primary production of *L. camara* increased considerably with decreasing tree density. If the number of patches is a meaningful estimate of *L. camara* population size in Mabira forest, it means that there is a positive relationship between sub-population size and the size of the largest individual within sub-populations. Thus, there is no indication that intra-specific competitions for light or other resources currently constrain plant size or the size of *L. camara* sub-populations within large gaps in Mabira forest. This further suggests that the size of these populations has the potential to increase in the future, potentially at the expense of the native flora within patches (Mauchamp et al., 1998; Islam et al., 2001).

The density of main branches of *L. camara* was positively related to gap size, meaning that *L. camara* develops more compact thickets in larger than in smaller gaps. One possible reason for this variation in growth pattern across the canopy size-gradient may be related to the variation in light availability among gaps

Fig. 2. Relationship between gap area and population dynamic parameters of *Lantana camara* in the Mabira forest-reserve in Uganda. Lines shown are significant ($P < 0.05$) linear regression lines. See Table 1 for statistical results.

of different sizes. The growth architecture of *L. camara* may affect species diversity beneath its canopy. In Mabira forest, we observed that patches of *L. camara* with a high branch density contain very little understorey vegetation, whereas patches with relatively low branch density commonly had some understorey species below their canopies (personal observation). Moreover, Islam et al. (2001) found that the invasion of *L. camara*, and other shrub species, into forest gaps after human disturbance cause an abrupt decline in species richness in tropical semi-evergreen forests of Bangladesh. Thus, it is possible that any negative effects of *L. camara* on the diversity of native understorey species are exaggerated in relatively large gaps, due to the more compact growth of *L. camara*-individuals there. More work is required to assess if the invasion of *L. camara* into canopy gaps of Mabira forest affects local species diversity.

The reproductive effort of *L. camara*, measured as the number of inflorescences per main branch, was positively related to gap size. Simultaneously, both branch density per patch and patch size was higher in large compared to small gaps, whereas the number of flowers and buds per inflorescence was unrelated to gap size. Therefore, the difference in total flower production per patch between relatively small and large gaps is substantially larger than the difference shown in Fig. 2G. Irrespective of the causal reason for this relationship, it shows that the reproductive output of *L. camara* potentially can be substantially higher in large compared to small gaps (since the number of patches per gap is also positively related to gap size). However, despite the positive relationship between gap size and reproductive effort, there was no relationship between the number of infructescences per main branch and gap size. In addition, the number of fruits per infructescence was not related to gap size. This result is consistent with Goulson and Derwent (2004), who found that fruit set per inflorescence in *L. camara,* was not related to the amount of shade falling on plants or habitat type. Even if we take into account the positive relationships between gap size, patch size, and branch density we found in Mabira forest, there is no relationship between the size of gaps and our estimate of reproductive output (number of infructescences) per patch. One possible reason for this lack of relationship may be that we obtained a static measure of the number of infructescences. It is possible that fruit removal rate by birds is higher in large than in small patches, causing the static number of infructescences to be independent of patch size, even if there is actually a positive relationship. Nevertheless, the positive relationship between gap size and the number of patches per gap results in a positive relationship between the total number of infructescences per gap and gap size ($P = 0.001$). Thus, *L. camara* sub-populations in relatively large gaps have a higher reproductive output than sub-populations in smaller gaps. This finding has consequences for the dispersal of *L. camara* in Mabira forest since relatively large gaps harbour sub-populations that may be particularly attractive to seed-dispersing birds. Individual gaps along trials may resemble fragments surrounded by a matrix of pristine tropical forest. These fragments are connected by trails functioning as corridors that dissect the forest interior. Since corridors may enhance seed dispersal by birds (Haddad et al., 2003), sub-populations within large gaps may function as sources that enhance population growth of sink sub-populations inside smaller gaps.

Although large gaps contain more *L. camara* flowers than smaller gaps, the pollinator visitation rate to inflorescences was unrelated to gap size. This suggests that the number of potential pollinators inside gaps is unrelated to gap size. However, it is highly possible that larger gaps contain more flower visitors than smaller gaps since the number of inflorescences is higher in large than in small gaps, and since there is no relationship between gap size and visitation frequency per inflorescence. It is, however, worth noting that this study was conducted over limited spatial and temporal scales. Based on our data, it is impossible to assess if there is any functional relationship between visitation frequency and the reproductive success of *L. camara*. However, in a study on *L. camara*-pollination in Australia, Goulson and Derwent (2004) found a strong positive relationship between the abundance of pollinators and fruit set, and several studies have found a positive relationship between population size and pollinator attraction and outcrossing rate in other species (e.g. Ågren, 1996; Ghazoul et al., 1998; Morgan, 1999; Wilcock and Neiland, 2002; Ghazoul and Shaanker, 2004). Thus, if there is a positive relationship between gap size and the number of *L. camara* genets per gap, it is conceivable that *L. camara* experience better cross-pollination opportunities in large compared to small gaps.

4.2. Management of Lantana camara in tropical forest gaps

With the goal of removing *L. camara* with minimal disturbance to the native forest biota, we recommend a programme for selective physical removal of *L. camara* individuals. After an initial removal-campaign of *L. camara*, resprouting shoots should be removed continuously, such that flowering is prevented. This may hinder a secondary spread of *L. camara* into naturally created gaps in the forest interior. In addition to a physical removal programme, shading in gaps should be restored by planting fast-growing native tree species with a dense canopy. Duggin and Gentle (1998) showed that shading by intact canopies is an effective barrier against successful invasion of *L. camara* as its regeneration is very poor below closed canopies. If gap-creation is unavoidable, for example because trails must be kept open for tourists, our results suggest that gaps should be made as small as possible, and attempts should be made to keep the canopy as closed as possible (see also Duggin and Gentle, 1998).

Ironically, *L. camara* is an important nectar source for several flower-visiting insects, such as bees and butterflies. Indeed, since flowering in several tropical species is sparse and individuals are often very isolated (Endress, 1996), the invasion of *L. camara* into forest-reserves may result in a continuous and easily accessible nectar source for flower visiting insects. This might be seen as an important resource for tropical forest-reserves since a high number and diversity of spectacular insects may attract tourists. This obviously contradicts our proposed goal of removing *L. camara*. In the case of controlling *L. camara* in Mabira Forest-reserve, managers therefore face the trade off between ecological and economical concerns. To resolve this issue, the reason for visitors coming to the forest should be critically assessed. If *L. camara* and associated flower visitors turn out to be unimportant for tourists, it can be removed without negative impacts on economic income. It may, however, be necessary to identify and promote the establishment of non-invasive native plants with flowering potentials that could maintain the biodiversity of pollinators associated with *L. camara*.

Acknowledgements

We are grateful for financial support from the Norwegian Council of Universities ‘Committee for Development Research and Education (NUFU, project no. 63/2003) through a grant to Kåre Lye, and the Norwegian Research council. We sincerely thank the Uganda Wildlife Authority and Uganda Forest Department for allowing us to work in Mabira forest-reserve and the Makerere University for hospitality. The Chief Manager of Mabira visitor centre, Ibrahim Senfuma, kindly guided us through the Mabira forest-reserve, and identified several plant species for us.

References

Ågren, J., 1996. Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. Ecology 77, 1779–1790.

Anon., 2000. Weeds of National Significanc (*Lantana camara*) Strategic Plan. National Weed Strategy Executive Committee, Launceston, Tasmania, Australia.

Anon., 2005. Global invasive species database, website: http://www.issg.org/database/species/ecology.asp%3F;si=56&fr=1%26;sts=

Ambika, S.R., Poornima, S., Palaniraj, R., Sati, S.C., Narwal, S.S., 2003. Allelopathic plants. 10. *Lantana camara* L. Allelopathy J. 12, 147–161.

Baldocci, D., Collineau, S., 1994. The physical nature of solar radiation in heterogeneous canopies: spatial and temporal attributes. In: Caldwell, M.M., Pearcy, R.W. (Eds.), Exploitation of Environmental Heterogeneity by Plants. Academic Press, New York, USA, pp. 21–71.

Barrows, E.M., 1976. Nectar robbing and pollination of *Lantana camara* (Verbenaceae). Biotropica 8, 132–135.

Cadenasso, M.L., Pickett, S.T.A., 2001. Effects of edge structure on the flux of species into forest interiors. Conserv. Biol. 15, 91–97.

Chandrasekaran, S., Swamy, P.S., 2002. Biomass, litterfall and aboveground net primary productivity of herbaceous communities in varied ecosystems at Kodayar in the western ghats of Tamil Nadu. Agric. Ecosyst. Environ. 88, 61–71.

Clark, D.A., Rich, P.M., Weiss, S., Oberbauer, S.F., 1996. Landscape scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rain forest. Can. J. Forest Res. 26, 747–757.

Daehler, C.C., 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annu. Rev. Ecol. Syst. 34, 183–211.

Drake, J.A., Mooney, H.A., Di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., Williams, M. (Eds.), 1989. Biological Invasions: A Global Perspective. John Wiley and Sons, Chichester, UK.

Duggin, J.A., Gentle, C.B., 1998. Experimental evidence on the importance of disturbance intensity for invasion of *Lantana camara* L. in dry rainforest-open forest ecotones in north-eastern NSW. Aust. Forest Ecol. Manag. 109, 279–292.

Endress, P.K., 1996. Diversity and Evolutionary Biology of Tropical Flowers. Cambridge University Press, Cambridge, UK.

Fensham, R.J., Fairfax, R.J., Cannell, R.J., 1994. The invasion of *Lantana camara* L. in Forty Mile Scrub National Park, north Queensland. Aust. J. Ecol. 19, 297–305.

Fine, P.V.A., 2002. The invasability of tropical forests by exotic plants. J. Trop. Ecol. 18, 687–705.

Gentle, C.B., Duggin, J.A., 1997. Allelopathy as a competitive strategy in persistent thickets of *Lantana camara* L. in three Australian forest communities. Plant Ecol. 132, 85–95.

Ghazoul, J., Shaanker, R.U., 2004. Sex in space: pollination among spatially isolated plants. Biotropica 36, 128–130.

Ghazoul, J., Liston, K.A., Boyle, T.J.B., 1998. Disturbance-induced density-dependent seed set in *Shorea siamensis* (Dipterocarpaceae), a tropical forest tree. J. Ecol. 86, 462–473.

Goulson, D., Derwent, L.C., 2004. Synergistic interactions between an exotic honeybee and an exotic weed: pollination of *Lantana camara* in Australia. Weed Res. 44, 195–202.

Haddad, N.M., Bowne, D.R., Cunningham, A., Danielson, B.J., Levey, D.J., Sargent, S., Spira, T., 2003. Corridor use by diverse taxa. Ecology 84, 609–615.

Hamilton, A.C., 1984. Deforestation in Uganda. Oxford University with the East African Wildlife Society, Nairobi, Kenya.

Holdgate, M.W., 1986. Summary and conclusions: characteristics and consequences of biological invasions. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 314, 733–742.

Horn, H.S., 1971. The Adaptive Geometry of Trees. Princeton University Press, Princeton, NJ, USA.

Islam, K.R., Ahmed, M.R., Bhuiyan, M.K., Badruddin, A., 2001. Deforestation effects on vegetative regeneration and soil quality in tropical semi-evergreen degraded and protected forests of Bangladesh. Land Degrad. Dev. 12, 45–56.

Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. 17, 164–170.

Lonsdale, W.M., 1999. Global patterns of plant invasion and the concept of invasibility. Ecology 80, 1522–1536.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and controls. Ecol. Appl. 103, 689–710.

Makana, J.R., Thomas, S.C., 2004. Dispersal limits natural recruitment of African mahoganies. Oikos 106, 67–72.

Mauchamp, A., Aldaz, I., Ortiz, E., Valdebenito, H., 1998. Threatened species, a re-evaluation of the status of eight endemic plants of the Galápagos. Biodivers. Conserv. 7, 97–107.

Mooney, H.A., 1999. Species without frontiers. Nature 397, 665–666.

Morgan, J.W., 1999. Effects of population size on seed production and germinability in an endangered, fragmented glassland plant. Conserv. Biol. 13, 266–273.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Syst. 10, 58–62.

Sharma, O.P., Makar, H.P.S., Dawra, R.K., 1988. A review of the noxious plant *Lantana camara*. Toxicon 26, 975–987.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M., Son, Y., 1999. Exotic plant species invade hot spots of native plant diversity. Ecol. Monogr. 69, 25–46.

Swaine, M.D., Withmore, T.C., 1988. On the definition of ecological species groups in tropical train forest. Vegetation 75, 81–86.

Usher, M.B., Kruger, F.J., MacDonald, I.A.W., Loope, L.L., Brockie, R.E., 1988. The ecology of biological invasions into nature reserves: an introduction. Biol. Conserv. 44, 1–8.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of earth's ecosystems. Science 277, 494–499.

Wilcock, C., Neiland, R., 2002. Pollination failure in plants: why it happens and when it matters. Trends Plant Sci. 7, 270–277.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperilled species in the United States. Bioscience 48, 607–615.

Williams, D.G., Mack, R.N., Black, R.A., 1995. Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. Ecology 76, 1569–1580.

Williamson, M., 1996. Biological Invasions. Clapman and Hall, London, UK, 244 pp.