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Rainfall and removal method influence eradication success for *Lantana camara*

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ABSTRACT

The success of invasive species eradication depends on a variety of factors, including those that initially facilitated the invasion, as well as removal and post-removal protocols. Two factors that appear to influence invasion by, and eradication of, the Neotropical shrub *Lantana camara* (L.), in southern Indian deciduous forests, are rainfall and removal method. However, their role in influencing eradication success is yet to be quantified, and remains unclear. We conducted an experiment to clarify how rainfall (high vs. low) and removal method (cutting vs. uprooting Lantana) influence re-invasion by Lantana, and native plant recovery. Rainfall influenced both eradication effort and outcomes – drier forest had lower starting levels of invader biomass, requiring less initial eradication effort, as well as lower subsequent Lantana re-invasion (from seed and rootstock) whereas wetter forest typically had greater starting levels of invader biomass, requiring considerably greater initial eradication effort, and greater Lantana re-invasion. However, wetter forest also showed greater native tree and forb recovery. Therefore, the availability of funds, local environmental gradients, and restoration priorities should inform the selection of restoration sites. With regard to removal method, uprooting combined with weeding of germinating Lantana, particularly after the rainy season, minimized overall re-invasion. Therefore, uprooting, followed by regular weeding of germinating Lantana and secondary invaders, is crucial to long-term Lantana eradication success.

Key words: invasion • rainfall • regeneration • tropical deciduous forest • uprooting • weeding

INTRODUCTION/CONTEXT

Ecological restoration, a key component in conservation efforts globally (Aronson and Alexander 2013), often includes the eradication of ecologically harmful invasive species (D'Antonio and Meyerson 2002). However, eradication success and native species recovery depend on site-specific factors, including the landscape variables and disturbance history that initially facilitated the invasion (Hobbs and Huenneke 1992; Duggin and Gentle 1998; Buckley et al. 2007), as well as removal and post-removal protocols (Flory and Clay 2009). Therefore, restoration plans almost always need to incorporate eradication protocols drawn from studies that address such factors.

Lantana camara (L.; Verbenaceae, hereafter Lantana), among the world's 100 most invasive species (Holm et al. 1991), is known to have diverse negative effects on native plant communities in several regions (e.g., Australia: Gooden et al. 2009a, b; India: Prasad 2010, 2012, Sundaram and Hiremath 2012; South Africa: Foxcroft and Richardson 2003; even North America: Langeland et al. 2011). It is a widespread weed in forests across India (Bhagat et al. 2012), and in southern Indian deciduous forests, is spreading at an alarming rate (Sundaram and Hiremath 2012). Two recent analyses suggest that invasion severity in India may be strongly linked to rainfall. The probability of encountering 'very dense' Lantana increased with increasing rainfall in the absence of fire (over an 18-year period within a rainfall range of 764–1840 mm per year; Ramaswami and Sukumar 2013), and moist deciduous forests had much higher Lantana stem densities than dry deciduous forests (Sundaram and Hiremath 2012). From a management perspective, these data suggest that eradication programs for Lantana may need to factor in rainfall.

Successful Lantana eradication has challenged managers globally for decades (Bhagat et al. 2012). Biocontrol is unreliable (Broughton 2000), and might have unintended (negative) effects on non-target species, which may be especially problematic in protected areas (Love et al. 2009). Burning Lantana *in situ* is a relatively recent phenomenon, the 'collateral' effects (on native vegetation) of which are not fully understood. Manual removal is the most common eradication approach in India (Bhagat et al. 2012), but its effectiveness and drawbacks are yet to be empirically understood.

It is widely but tacitly known among managers and researchers in India that (a) cutting Lantana aboveground, the most common removal practice in India, exacerbates the invasion by facilitating aggressive re-growth from the root-stock (Love et al. 2009), and (b) removing the root-stock can prevent

Lantana from resprouting (Babu et al. 2009). Because uprooting is more time- and labor-intensive, forest managers have mostly cut Lantana, leaving the root-stock intact. However, there has been no systematic monitoring of the consequences of this management approach for either Lantana or native plants, even while many recognize that it may intensify subsequent re-invasion. In this study, we address these gaps in our understanding of Lantana eradication by experimentally evaluating how rainfall (high vs. low) and removal method (cutting vs. uprooting) influence both recolonization by Lantana and native plant recovery.

Study Methods — To clarify the influence of rainfall and removal method on Lantana eradication success, we conducted a small-scale, 16-month (February 2012 to May 2013) experiment in Mudumalai Tiger Reserve (MTR; 321 km^2; 11°30′ N, 76°30′ E – 11°42′ N, 76°45′ E), in southern India. MTR has two periods of rainfall – June–August (south-west monsoon), and November–December (north-east monsoon). MTR also lies along an east-west rainfall gradient (~ 700 to ~ 1700 mm annual average; Weather station, Centre for Ecological Sciences, Indian Institute of Science (CES-IISc)) which results in a gradient of forest types – thorn scrub forest in the east, semi-evergreen and moist deciduous forest in the west, and dry deciduous forest in between (Sharma et al. 1977). In recent years, the understory of the dry deciduous forest, where tallgrasses (including *Themeda* spp.; Poaceae) were the dominant native vegetation, has been extensively invaded by non-native plants (including *Chromalaena odorata* (L.) R. M. King and H. Rob and *Parthenium hysterophorus* (L.); Asteraceae) of which Lantana is the most abundant – in some sites dry, above-ground Lantana biomass exceeds 5 kg/m^2 (Prasad 2012).

We selected two sites, approximately 9.7 km apart, differing in their average annual rainfall, for experimental Lantana removal. The low rainfall (hereafter LR; 11°37′ N, 76°37′ E) site receives 867 ± 73 mm of rain annually (averaged over the last 10 years; range: 450–1231 mm), while the high rainfall (hereafter HR; 11°34′ N, 76°32′ E) site receives 1295 ± 87 mm (range: 1002–1648 mm; CES-IISc). Discussions with managers of MTR, and reconnaissance visits to the two sites, revealed that they were otherwise similar in geology and topography, tourism (absent), management (including clearing of vegetation within firebreaks), and disturbance (livestock grazing, firewood harvest, and other human forest-resource extraction activities absent). Both sites were also bisected by a 10-m-wide management road, with dense Lantana thickets on either side. At each site, we established 48 plots (5 m × 5 m; n = 96) within these thickets, distributed equally across three plot types – Cut plots (wherein Lantana was cut but the root-stock was left intact), Uproot plots (wherein the root-stock was also removed), and Control plots (wherein no Lantana was removed) – and on both sides of the road. Plots were approximately 10-15 m apart, and approximately 5 m from the road verge. Thus, at each site, eight plots of each type were located on each side of the road, with Control plots located between plots assigned to each removal treatment.

Before applying experimental treatments, we estimated initial Lantana biomass (kg/m^2) by cutting, drying, and weighing all above-ground Lantana (regardless of where it was rooted) that occurred within the bounds of a randomly-placed 1-m × 1-m quadrat in each plot (for detailed methods and rationale for using biomass as a measure of abundance, rather than stem counts, refer to Prasad 2012). Immediately following Lantana removal (in February 2012), we monitored (a) the abundance of native understory vegetation (densities for tree seedlings, tree saplings and forbs, and grass cover (% area covered by grass)) in all plots, and (b) colonization by the three most abundant exotic plants in this system (viz., Lantana, *C. odorata*, and *P. hysterophorus*) in each Cut and Uproot plot, by counting (and subsequently weeding) all seedlings of these species. We conducted a total of four rounds of monitoring (May 2012, September 2012, January 2013, and May 2013), over a 16-month period. In the final round of weeding and monitoring, in May 2013, we also re-estimated Lantana biomass (kg/m^2) within randomly-placed 1-m × 1-m quadrats in all plots.

We used linear mixed models to compare initial (February 2012) values of Lantana biomass and native plant abundance (grass cover and densities of forbs, tree seedlings and saplings) between sites and across treatments, with rainfall (LR and HR) and removal method (Cut, Uproot) included as fixed effects and plots as the random effect. We used the R package `lmerTest` for our analysis, and tested the statistical significance of fixed effects using Type III ANOVAs based on Satterthwaite approximations for the degrees of freedom (Kuznetsova et al. 2015). Similar linear mixed models were used to compare final (May 2013) values of Lantana biomass and native plant abundance (grass cover and densities of tree seedlings and saplings, adult forbs and forb seedlings) between sites and across treatments, with rainfall (LR and HR) and treatment (Cut, Uproot and Control) included as fixed effects and plots as the random effect. However, by the end of the experiment, plots assigned the Uproot treatment had no Lantana present. To avoid issues arising from non-homogeneity of variances, we, therefore, included only Control and Cut plots for our final comparison of Lantana biomass. Lantana biomass and tree seedling density data from both censuses, and forb seedling and adult forb densities from the initial census (February 2012) were square root transformed to meet model assumptions. Initial adult forb densities in one plot assigned the Cut treatment were exceptionally high compared to the rest of the plots, and was dropped from the analysis. Inspection of residual plots indicated that models were well behaved in all cases.

We also used Generalized Linear Mixed Models (GLMM) to evaluate the effectiveness of removal method on germination of the three exotic species – Lantana, *C. odorata*, and *P. hysterophorus* – at the LR and HR sites. Rainfall and removal method were included as fixed effects, with plots and time included as random effects to account for the non-independence of repeated measures within plots over time. Analyses were carried out using the `lme4` package, and the `car` package was used to conduct Type II Wald chi-square tests, to assess the statistical significance of the fixed effects (Bates et al. 2017). We used a GLMM with Poisson errors for the analysis of Lantana seedling data, and a negative binomial GLMM for the *C. odorata* data. We were unable to get the model for *P. hysterophorus* to converge (it germinated almost exclusively at the LR site), and so report only summary statistics for this species. All analyses were conducted using R version 3.2.4 (The R Foundation for Statistical Computing, 2016).

RESULTS

Differences between initial vegetation at high and low rainfall sites — At the start of the experiment, Lantana biomass (± 1 SE kg/m^2) was significantly higher at the HR site ($F_{1, 27.3} = 11.11$, $p = 0.002$), which had, on average, 40% more Lantana biomass (2.74 ± 0.14) than the LR site (1.96 ± 0.14). Within sites, there was no difference in Lantana biomass between plots assigned either removal treatment at the HR site (2.58 ± 0.25 vs 2.89 ± 0.29 in Uproot vs Cut, respectively), but at the LR site, plots assigned the Uproot treatment supported lower initial Lantana biomass on average compared to plots assigned the Cut treatment (1.45 ± 0.18 vs 2.47 ± 0.27 kg/m^2, respectively; Rainfall x Treatment: $F_{1,27.3} = 8.04$, $p = 0.008$). Conversely, the density of some native plants was significantly lower in the HR site compared to the LR site at the start of the experiment, including adult forbs (0.12 ± 0.15 vs 1.14 ± 0.9 per m^2 respectively; $F_{1,29.8} = 94.2$, $p < 0.0001$) and forb seedlings (0.06 ± 0.02 vs 0.64 ± 0.11 per m^2 respectively; $F_{1,58} = 38.1$, $p < 0.0001$), but not across plots assigned different treatments at each site (Treatment and Treatment x Rainfall interactions not significant in both cases). Tree sapling densities were similarly marginally lower at the HR site compared to the LR site (12.3 ± 2.1 vs 7.8 ± 1.22 per m^2; $F_{1,58} = 3.48$, $p = 0.06$), but did not differ across plots assigned different treatments ($F_{1,58} = 1.07$, $p = 0.31$). Grass cover and tree seedling densities at the start did not differ between sites or plots assigned different removal treatments.

Relationship between rainfall and Lantana regrowth— At the end of the 16-month experiment, Lantana was absent in all the plots assigned the Uproot treatment, at both sites. Lantana biomass in Cut plots was significantly lower than that in Control plots, although the magnitude of the difference differed between the LR and HR sites (Rainfall x Treatment: $F_{1,58} = 5.733$, $p = 0.02$). Cut plots experienced ~18 % and 57 % regrowth from root-stock in LR and HR plots, respectively. Overall, Lantana biomass in Cut plots was ~ 2.5 times higher at the HR site (0.98 ± 0.15 kg/m^2) compared to the LR site (0.40 ± 0.08 kg/m^2; Fig. 1).

Effects of removal method on germination of Lantana and other exotic plants — Although Lantana removal triggered the germination of all three exotic invasive plants, germination was not influenced by method of Lantana removal (Lantana: $\chi^2 = 0.26$, df = 1, $p = 0.61$; *C. odorata*: $\chi^2 = 0.04$, df = 1, $p = 0.82$; *P. hysterophorus*: $\chi^2 = 0.255$, df = 1, $p = 0.61$; Fig. 2). Pooled over both removal treatments (to isolate the effect of rainfall), Lantana germination was 75 % higher in the HR site (192 ± 21 seedlings/plot) than in the LR site (109 ± 18; $\chi^2 = 665.4$, df = 1, $p < 0.001$). *C. odorata* germination was also significantly higher ($\chi^2 = 98.7$, df = 1, $p < 0.001$) in the HR site (331 ± 76) than in the LR site (28 ± 5). In contrast, *P. hysterophorus* germination occurred almost entirely in the LR site (81 ± 1.8), with no germination observed in any Uproot plots, and little to no germination observed in most Cut plots at the HR site (4 ± 0.7). Finally, whereas Lantana and *C. odorata* germination peaked following the south-west monsoon (in September), *P. hysterophorus* germination peaked following the north-east monsoon (in January).

Response of native plants — At the end of the 16-month study, there were no differences in native tree sapling ($F_{2,87} = 0.285$, $p = 0.75$) or adult forb ($F_{2,87} = 1.262$, $p = 0.28$) densities between plots assigned Cut, Uproot, and Control treatments, at either LR or HR site (Appendix 1). However, at both the HR and LR sites, Lantana removal per se (by either method) resulted in greater seedling regeneration for both trees (Treatment: $F_{1,42.8} = 5.08$, $p = 0.03$, Site: $F_{1,68.4} = 8.9$, $p = 0.004$) and forbs (Treatment: $F_{1,38.7} = 5.05$, $p = 0.02$; Site: $F_{1,65.5} = 4.88$, $p = 0.03$). Relative to Control plots, tree seedling densities were ~ 2.5 times greater in plots where Lantana had been removed (Cut and Uproot pooled to isolate the influence of rainfall) at the LR site (0.17 ± 0.04 vs 0.05 ± 0.02 per m^2, respectively) and nearly 4 times higher at the HR site (0.51 ± 0.12 vs 0.13 ± 0.05 per m^2, respectively), while forb seedling densities were ~1.5 times greater in removal plots at the LR site (40.6 ± 4.2 vs 27.8 ± 4.2 per m^2, respectively) and ~1.8 times higher at the HR site (37.3 ± 7.7 vs 20.2 ± 5.2 per m^2, respectively).

Removal treatments also significantly impacted grass cover ($F_{2,45.1} = 8.46$, $p < 0.001$), with similar responses observed at both the low and high rainfall sites (Treatment x Rainfall: $F_{2,44.7} = 0.998$, $p = 0.38$). Overall, grass cover was higher in the LR site compared to the HR site (21.6 % vs 12.9 % pooled across all treatments at the LR and HR sites, respectively; $F_{1, 44.7} = 14.86$, $p < 0.001$). At both the LR and HR sites, grass cover was highest in the Uproot plots, followed by the Cut plots and the Controls (Appendix 1). On average, Lantana removal per se (by either method) resulted in a near doubling of grass cover in sites ($F_{1,39.5} = 11.45$, $p = 0.002$; LR: 13.3 ± 2.8 % in control vs 25.8 ± 3.1 in removal plots; HR: 8.1± 1.5 % in control vs 15.2 ± 1.4% in removal plots).

DISCUSSION

The selection of restoration sites must take into consideration the pros and cons of high and low rainfall scenarios for both exotic and native plants. In this study, native plant recovery (tree and forb seedling germination) was greater in the wetter site when compared to the relatively dry site. However, both initial Lantana abundance and re-invasion from rootstock, as well as Lantana and *C. odorata* germination, were also higher in the wetter site. Considering that the adverse impacts of Lantana on native plants increase with increasing Lantana abundance (Prasad 2012), which is greater in wetter forest, high rainfall sites appear to offer greater returns for restoration effort in terms of reducing the impact of Lantana on, and facilitating the subsequent recovery of, native trees and forbs.

On the other hand, although native understory recovery was not particularly noteworthy in the low rainfall site, both initial Lantana biomass (to be uprooted at the beginning of restoration efforts) as well as Lantana re-invasion, both from root-stock and seed (to be subsequently weeded seasonally), were lower than in high rainfall areas. Therefore, the effort and expense required to maintain Lantana-free forest in low rainfall areas would be considerably lower than in areas with relatively high rainfall. The selection of restoration sites will, therefore, depend on local environmental factors, restoration priorities and challenges, and the availability of funds.

Our study, the first to quantitatively compare common mechanical removal methods for Lantana, supports anecdotal knowledge of differences in efficacy between the methods. When cut, Lantana re-sprouts vigorously from root-stock (as reported by Love et al. 2009 for northern Indian sites), thereby requiring repeated cutting, and consequently greater long-term investment. Uprooting, on the other hand, takes greater initial investment (time and labor) but kills the plant, thus reducing long-term expenditure. The study also highlights the importance of systematic, ongoing weeding of Lantana for minimizing aggressive Lantana re-invasion (Ramaswami et al. 2014), and promoting native seedling establishment (Raman et al. 2009). The initial effort of eradicating invasive plants, which is often substantial, can be futile if resources are not available to ensure long-term success and sustainability (Norton 2009). Continued follow-up management and monitoring are essential but most often absent from restoration practice (D'Antonio and Meyerson 2002). In the case of Lantana, after the initial uprooting effort, follow-up weeding for several seasons may be imperative to localized long-term eradication success and native plant community recovery. Our data suggest that such weeding should be carried out during peak germination periods immediately following rains, when the largest numbers of 'invader' seedlings can be removed, and uprooting them is relatively easy because the ground is damp.

Based on our findings we recommend that practitioners consider the following when developing invasive plant eradication programs: (1) environmental gradients such as rainfall (which may result in large differences in the cost and success of invader eradication, and subsequent native species recovery), must be built into restoration programs within invaded landscapes; (2) the specific technique used to remove the invader could make all the difference between successfully eradicating it and increasing its abundance; (3) seasonal variation in the responses of critical life-stages, such as germination or fruiting peaks, may provide windows that can be exploited for eradication interventions such as weeding; and (4) as a general rule, greater initial investments in restoration efforts can result in greater long-term pay offs.

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FIGURES

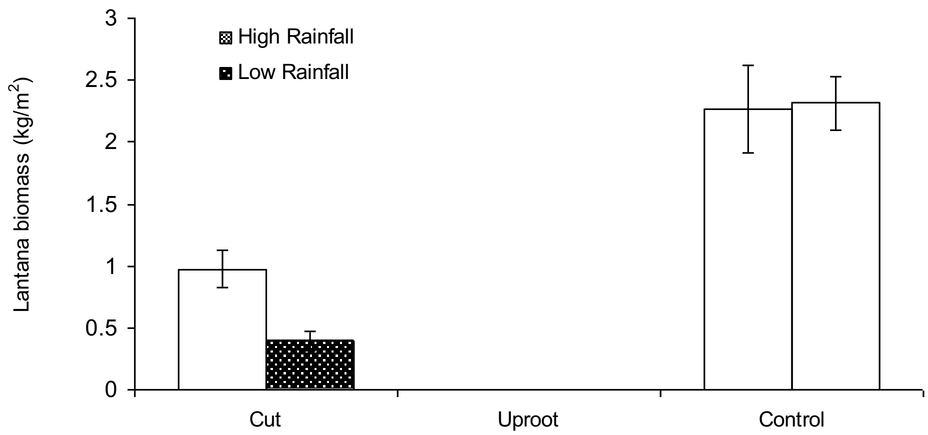


Figure 1. Final (May 2013) dried, above-ground Lantana biomass in plots across three treatments (Cut, Uproot, and Control) and across two sites differing in rainfall – low rainfall and high rainfall. Initial values of biomass did not differ between plots assigned to different removal treatments. Data from 93 plots in Mudumalai Tiger Reserve, southern India.

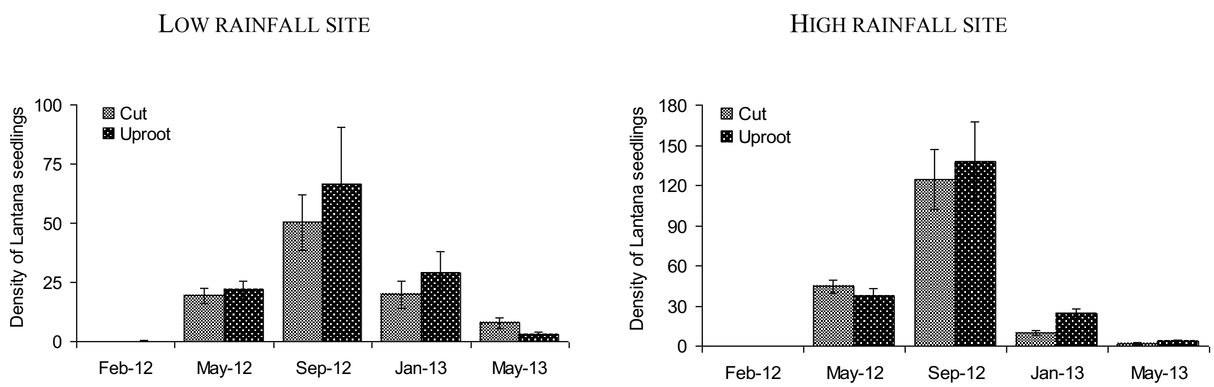
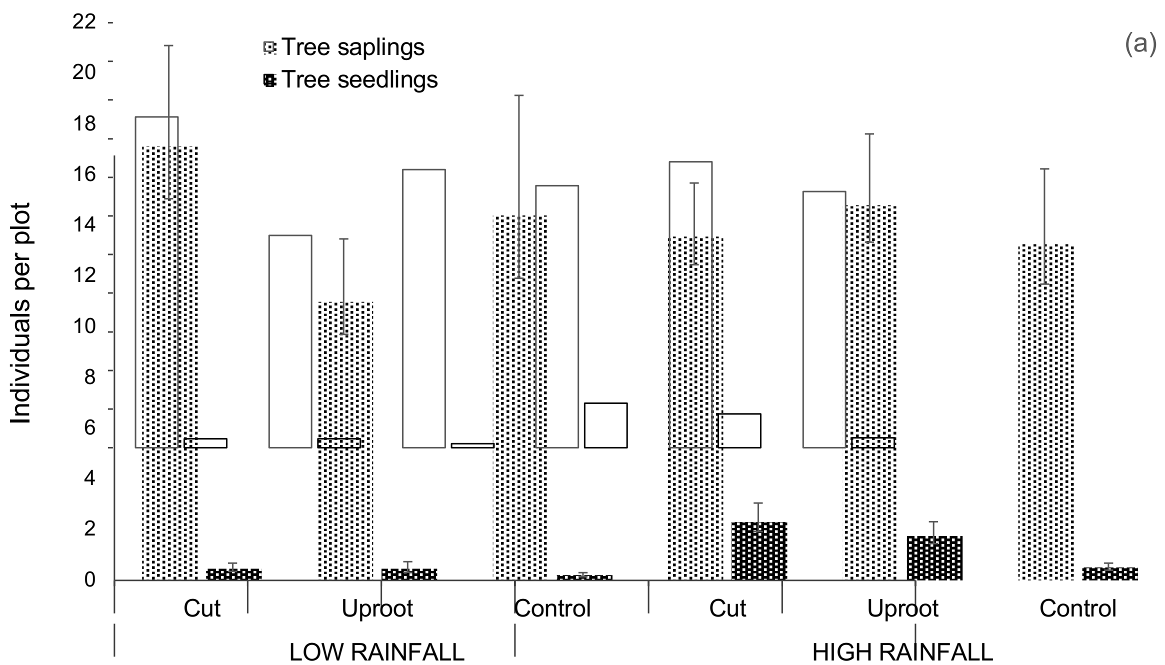


Figure 2. Lantana germination after the removal of Lantana by one of 2 methods – cutting or uprooting – monitored across 5 seasons at two deciduous forest sites varying in average annual rainfall – Low Rainfall (n = 30 plots), and High Rainfall (n = 32 plots) in Mudumalai Tiger Reserve, southern India.

APPENDIX 1



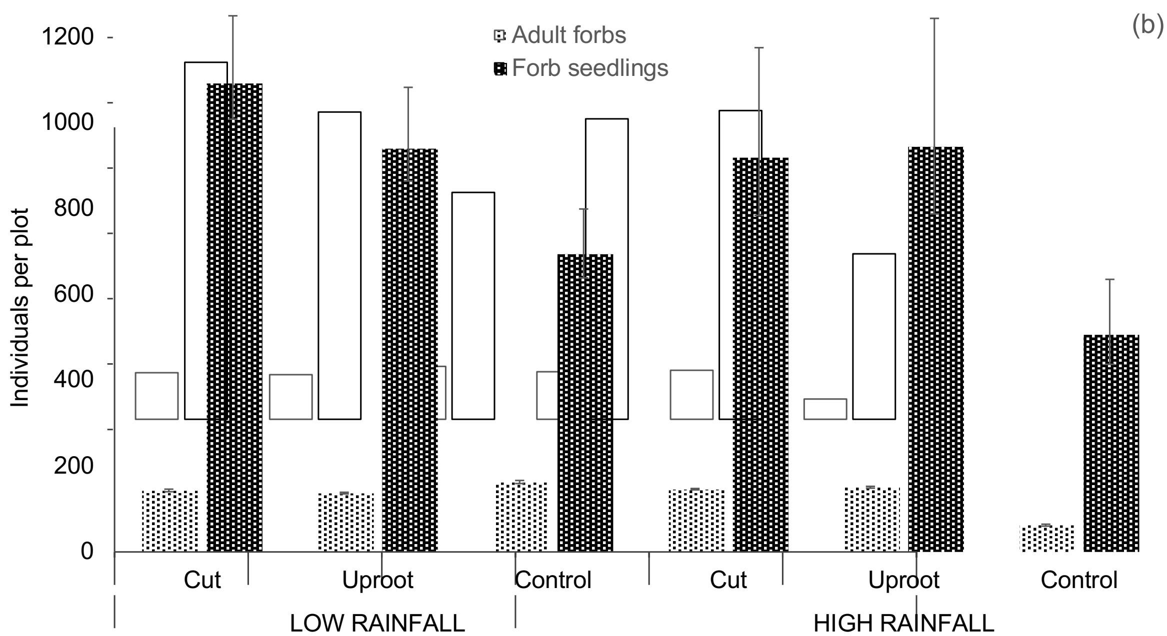


Figure 1. Regeneration of native understory plants – (a) trees (saplings and seedlings) and (b) forbs (adults and seedlings) – 16 months after experimental Lantana removal, in 5-m × 5-m plots assigned to one of three Lantana removal treatments (Cut, Uproot, and Control) at two sites differing in mean annual rainfall (Low Rainfall and High Rainfall). Data are from 93 plots in the deciduous forests of Mudumalai Tiger Reserve, southern India.

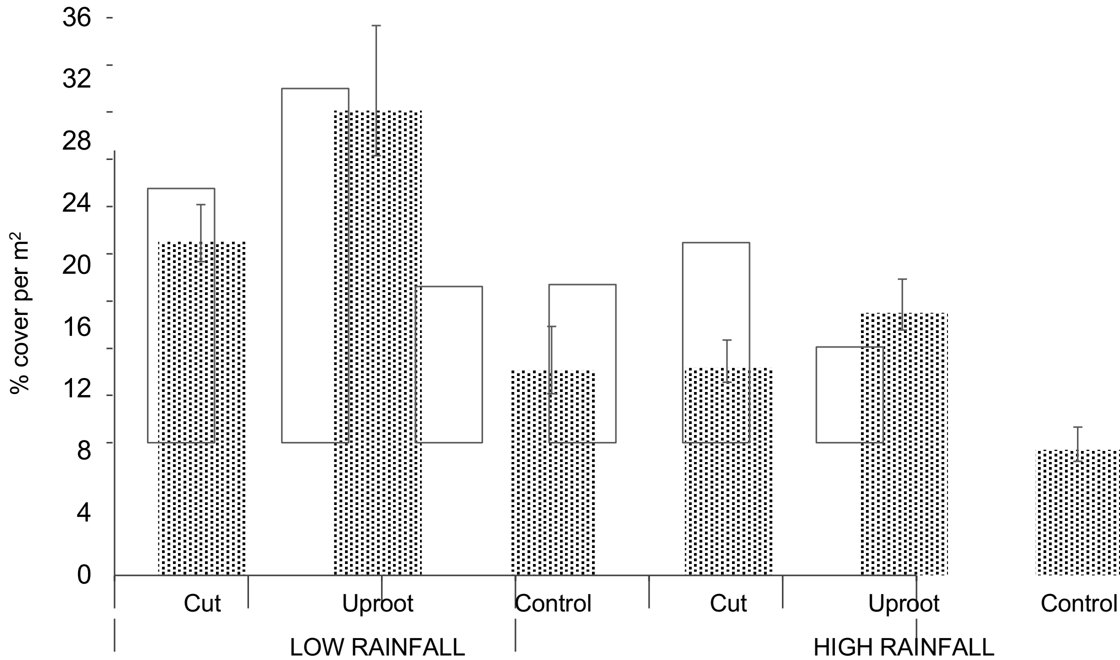


Figure 2. Grass cover, 16 months after experimental Lantana removal, in 5-m × 5-m plots assigned to one of three Lantana removal treatments (Cut, Uproot, and Control) at two sites differing in mean annual rainfall (Low Rainfall and High Rainfall). Data are from 93 plots in the deciduous forests of Mudumalai Tiger Reserve, southern India.