

Research Article

Artificial perches and solarization for forest restoration: assessment of their value

Aline Luiza Tomazi^{1,2} and Tânia Tarabini Castellani¹

¹ Programa de Pós-Graduação em Ecologia, Departamento de Ecologia e Zoologia, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina, Campus Universitário, 88040-900, Florianópolis/SC, Brasil.

² Corresponding author email address: A. L. Tomazi, email aline_luiza_05@hotmail.com.

Abstract

Artificial perches have been considered an effective way to increase the influx of zoochoric seeds on degraded areas. A main barrier to seedling recruitment beneath perches is competition with other plants, including non-native or invasive species. We therefore believed that the seedling recruitment would increase with invasive species management through solarization. We assessed the use of artificial perches combined with solarization as a management technique for forest restoration. An outline of subdivided plots was installed in an abandoned pasture originally covered by subtropical Atlantic forest in southern Brazil. The invasive species were Nutgrass (*Cyperus rotundus* - Cyperaceae) and African Liverseed Grass (*Urochloa arrecta* - Poaceae). Solarization was achieved using a black polyethylene cover. Artificial perches were installed after solarization was complete. Seed rain and established plant community species were assessed. Solarization initially eliminated previously existing vegetation, but the effects were not long lasting. Invasive species grew aggressively by vegetative means from the borders of solarized areas. Artificial perches increased the influx of zoochoric seeds, but the seeds were unable to germinate and establish due to competition by the fast growing invasive species. The combined use of artificial perches and solarization for forest restoration seems to have limited effectiveness.

Key words: *Cyperus rotundus*, degraded area, invasive species control, *Urochloa arrecta*, zoochory.

Resumo

Poleiros artificiais têm sido considerados efetivos em incrementar o fluxo de sementes zoocóricas para áreas degradadas. Contudo, uma das maiores barreiras para o recrutamento de plântulas sob os poleiros artificiais é o efeito da competição com outras plantas, incluindo espécies não nativas e/ou invasoras. Acreditamos então que o recrutamento destas plântulas poderia ser incrementado com o manejo das espécies invasoras através da solarização. Empregamos em nossa pesquisa poleiros artificiais combinados com solarização, como técnicas de manejo para a restauração florestal. Um delineamento de parcelas subdivididas foi instalado em uma pastagem abandonada originalmente ocupada por Floresta Atlântica em clima subtropical no sul do Brasil. As espécies invasoras foram a tiririca (*Cyperus rotundus* - Cyperaceae) e a braquiária (*Urochloa arrecta* - Poaceae). A solarização foi aplicada com camadas de polietileno preto. Os poleiros artificiais foram instalados após o término da solarização. A chuva de sementes e as espécies estabelecidas na comunidade vegetal foram avaliadas. A solarização eliminou inicialmente a vegetação pré-existente, porém os efeitos não foram duradouros. As espécies invasoras apresentaram um crescimento agressivo por meio vegetativo a partir das bordas das áreas solarizadas. Os poleiros artificiais incrementaram o fluxo de sementes zoocóricas, mas estas sementes não conseguiram se estabelecer devido à competição com as espécies invasoras que rapidamente invadiram as áreas solarizadas. O uso de poleiros artificiais combinado com a solarização para a restauração florestal parece ser limitado.

Palavras-chave: Área degradada, controle de espécies invasoras, *Cyperus rotundus*, *Urochloa arrecta*, zoocoria

Received: 28 February 2016; **Accepted** 2 May 2016; **Published:** 27 June 2016

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Cite this paper as: Tomazi, A. L. and Tarabini Castellani, T. 2016. Artificial perches and solarization for forest restoration: assessment of their value. *Tropical Conservation Science* Vol. 9 (2): 809-831. Available online: www.tropicalconservationscience.org

Disclosure: Neither Tropical Conservation Science (TCS) or the reviewers participating in the peer review process have an editorial influence or control over the content that is produced by the authors that publish in TCS.

Introduction

Seed limitation is an important factor defining the structure of plant communities, and is therefore of fundamental interest in ecological restoration [1]. This limitation restricts species' abilities to reach recruitment sites [2], a main barrier to the restoration of degraded tropical environments [3]. This might be the result of "limited sources", where insufficient seeds are produced to saturate all potential recruitment sites; or of "limited dispersal", when dispersal agents are insufficient despite the production of large seed quantities [4].

Artificial perches have been used as a low cost technique in restoration [5], and are efficient in attracting dispersal agents to degraded areas [6-8]. The structures imitate dry vegetation branches, creating propitious landing spots for potential seed-dispersing birds, which defecate or regurgitate seeds from adjacent areas, potentially increasing local regeneration and development of plant communities [5].

The recruitment of seed dispersed beneath artificial perches is, however, often reduced compared to the seed rain attracted [3, 9-10-]. Recruitment of these seedlings may be prevented by adverse micro-climatic conditions, low soil nutrient availability, low seed viability, seed predation [11], or competition from other plants, especially non-native and invasive species [3, 6, 11]. Seedling recruitment beneath artificial perches may therefore be increased by combining perches with non-native and invasive plant management and other restoration methods [12]. One option is to combine artificial perches with solarization, which removes competition from non-native and invasive species [13-14].

Non-native and invasive species affect the composition and functioning of a community by altering ecological interactions [15], species richness, species diversity, and species composition [16-17], thus greatly complicating restoration efforts [17-18]. Non-native and invasive species have been traditionally managed in restoration areas with the use of herbicides [12, 19], controlled burning [120], trimming or clearing [21], tilling [14], or shading by vegetation [22]. These control methods may become expensive when repeated operations are required [14].

Solarization, commonly used in agriculture [23], has been effective in the restoration of degraded prairies and low forests in Mediterranean and/or temperate climates [14, 24-29] and tropical moist lowland forest [13]. Solarization involves covering damp soil with an isolating layer of transparent or black polyethylene, which is heated by sunlight and, when black, restricts the passage of light, inhibiting species growth [14, 30]. The seed bank and subterranean propagules (rhizomes, bulbs and tuberous roots) are depleted, facilitating the establishment of desired species and avoiding the need for repeated management [14, 25, 31]. Despite the

potential of solarization for restoring degraded areas, its use combined with artificial perches has not been tested in scientific literature.

In this study we assess the use of solarization combined with artificial perches in the restoration of a degraded pasture area with a high incidence of invasive species (Nutgrass - *Cyperus rotundus* – Cyperaceae, and African Liverseed Grass - *Urochloa arrecta*- Poaceae) in the subtropical Atlantic Forest of Brazil. We posed the following questions: (1) What are the short-term effects (immediately after implementation) and long-term effects (one year after implementation) of solarization on invasive and on other species in the plant community? (2) Do the artificial perches increase the influx of zoochoric seeds? (3) What are the effects of the combined use of artificial perches and solarization in the development of a plant community in forest restoration? We hypothesized that solarization would eliminate ground vegetation cover (invasive and other species) immediately, and artificial perches installed after solarization would attract a greater influx of zoochoric seeds, which would then be able to establish, accelerating the restoration of the plant community.

Methods

Study area

The study was undertaken in southern Brazil, in the City of Tijucas, Santa Catarina State, (27° 15' 48" S and 48° 44' 49" W – Fig. 1), in the subtropical Atlantic Forest of Brazil classified as Dense Ombrophilous Forest [32]. The climate is subtropical, altitude 15 m a.s.l., mean annual temperature 23°C, and mean annual rainfall 1,600 mm [33]. The study site is located in a disturbed vegetation matrix on a plain of damp clay soil that undergoes temporary flooding. Soil use and management in a 500 m radius include forestry with *Eucalyptus* sp., pasture, agriculture, and three small (<10ha) secondary forest fragments. These fragments function as potential propagule sources for regeneration of the study site (at least pioneer trees and shrubs species with rapid growth) as they are located within 100m.



Fig.1. Map indicating the location of the study area in Tijucas City, Santa Catarina State, Brazil.

The original vegetation in the restoration area was eliminated to be used as pasture over 40 years ago. Then it was left abandoned for about 15 years, with occasional vegetation trimming until the study started in 2011. There were no burning or fire events during the time of abandonment. The herbaceous perennials and non-native invasive species Nutgrass and African Liverseed Grass dominated the area, amongst few other

regenerating species. Both invasive species are cited in literature as vigorous reproducers, especially by vegetative means [34-35]. Nutgrass stores energy in underground rhizomes, bulbs, and tuberous roots, which allow the plants to recover quickly after disturbance [34], while African Liverseed Grass resprouts vigorously from aerial stolons [35]. No shrubs or trees with structures or branches that might attract potential seed dispersers were present.

Experimental design and treatments

In July, 2011, the vegetation in the study site was removed with a hand trimmer, leaving all underground vegetative structures. We then used solarization and artificial perch treatments in split plots in accordance with Gotelli & Ellison [36], as follows: (1) solarization treatment (full plot factor) – solarized and unsolarized; (2) artificial perch treatment (subplot factor) – with artificial perches and without artificial perches (designated as open field). The solarization treatment was applied to twenty 4 x 11 m plots (10 solarized and 10 unsolarized) at least 4 m apart (Appendix 1). The artificial perch treatment was applied to each plot, with 20 artificial perches (10 in solarized plots and 10 in unsolarized plots). We placed perches on the right or left side of split plots at random (Appendix 1), defining the opposite sides as open field. One seed collector was installed in each plot beneath artificial perches and one in each open field plot. One vegetation monitoring plot was also set up in each artificial perch plot and in its corresponding open field area. Both seed collectors and vegetation monitoring plots were also placed at random (Appendix 1). The collectors, made of wood and 100% polyester cloth, stood approximately 0.5 m above the ground. A total of 40 square seed collectors measuring 0.5 m² each and 40 permanent square monitoring plots measuring 1 m² each were set up. Each artificial perch was installed 2 m from plot borders. In accordance with Shiels & Walker [11], a minimum distance of 4 m was kept between seed collectors and vegetation monitoring plots beneath artificial perches and in open field to ensure sampling independence (Appendix 1).

In August, 2011, the plots were subjected to solarization under black polyethylene, in accordance with Marushia & Allen [14], and Grose [27]. We used black rather than transparent polyethylene because it was cheaper and in previous tests more effectively inhibited those invasive species. Solarization plots were covered by three layers of 15 µm black polyethylene fixed to the ground using bricks. Because the soil was naturally damp, it was not previously irrigated as is often done in solarization [37]. After 113 days, in December, 2011, the polyethylene cover was removed. The solarization period was similar to the one used by Wilson et al. [24].

Artificial perches were installed in January, 2012, 23 days after polyethylene removal. Structures were made of 2 m high bamboo stems with a perpendicular beam on top made of bamboo branches for bird perching, in accordance with Shiels & Walker [11] and Tomazi et al. [38]. Each artificial perch was placed between seed collector and vegetation monitoring plots to ensure the branches extended over both.

Monitoring seed rain and development of plant community

We monitored seed rain underneath artificial perches and in open field every fortnight between January and December, 2012. The seeds collected were separated in morphotypes, identified when possible by comparison with seeds collected in the surroundings or by specialized literature and experts, and quantified.

The development of plant community was monitored every three months in five sampling phases, the first in December, 2011 (after removing solarization polyethylene and before installing artificial perches), and again in March, June, and October, 2012, and January, 2013. Using the point quadrat method [39], we quantitatively assessed percentage cover and cover repetition of the invasive species Nutgrass and African Liverseed Grass and of all species beyond average foliage height established in the plots by seed germination or vegetative propagation. According to the point quadrat method [39], we evaluated 25 points in each 1m² plot, totaling 1,000 points in each sampling period. An iron rod (0.5cm in diameter, 2m high) was vertically placed in vegetation, and all intercepted species were registered. We also counted the total number of intercepts between each species and the rod and the class height of these contacts: (1=0.00-0.25; 2=0.26-0.50; 3=0.51-1.00; 4=1.01-1.25; 5=1.26-1.50; 6=1.51-1.75; 7=1.76-2.00; 8=above 2.00 m). These data were used to calculate percentage cover, cover repetition, and weighted average height for each invasive species and other species of the plant community.

The species found in seed rain and in vegetation monitoring plots were classified, when possible, according to dispersal syndrome [40], life form, and origin [41-42].

Data analysis

Percentage cover (PCi), cover repetition (Rci), and average height (Ai) were calculated for the invasive species Nutgrass and African Liverseed Grass and all other species. The formulas used were according to Goodal [39] and are presented in Appendix 2.

We used the Wilcoxon-Mann-Whitney (U Test) to assess the short-term effects of solarization on invasive and all other plant community species. We performed an Analysis of Variance (ANOVA) of repeated measures followed by Tukey's Honest Significant Difference Test (HSD) to check how long the solarization effects on invasive species had persisted throughout the year. We developed species accumulation curves (Mao Tau) [43] to verify differences in seed rain beneath artificial perches and in open field. To test the difference in vegetation species composition between applied treatments we also built species accumulation curves (Mao Tau) [43] and Individual Indicator Value Test (IndVal) [44]. We performed an Analysis of Variance (ANOVA) of split plots followed by Tukey's Honest Significant Difference Test (HSD) to analyze the effects of the combined use of artificial perches and solarization on development of the plant community. We used EstimateS version 7.5.2 [43] and R version 2.15.0 [45] software for statistical analyses.

Results

Short effects of solarization on invasive and on all others species

Solarization initially removed the invasive species Nutgrass and African Liverseed Grass and all other plants. Shortly after removal of the solarization polyethylene cover, the plots subjected to this treatment showed percentage cover values at or near zero cover repetition and height for Nutgrass and African Liverseed Grass, as well as all other plants compared to unsolarized plots (Table 1).

Table 1. Median (min-max) of descriptive variables of invasive species and other plant community species immediately after (short-term effects) removal of solarization polyethylene. Values followed by different letters represent statistical differences determined by the U Test, where: Sol - = unsolarized, and Sol + = solarized.

		Nutgrass <i>Cyperus rotundus</i>		African Liverseed Grass <i>Urochloa arrecta</i>		Others species	
		Sol -	Sol +	Sol -	Sol +	Sol -	Sol +
Percentage cover	Median	51 ^{a***}	0 ^{b***}	51 ^{a***}	0 ^{b***}	68 ^{a***}	2 ^{b***}
	Min-Max	(0-94)	(0-0)	(2-78)	(0-4)	(32-90)	(0-12)
	Test	W ₁₀ =95		W ₁₀ =97.5		W ₁₀ =100	
Cover repetition	Median	1.3 ^{a***}	0 ^{b***}	0.9 ^{a***}	0 ^{b***}	3.7 ^{a***}	0.1 ^{b***}
	Min-Max	(0-2.8)	(0-0)	(0-2.2)	(0-0.1)	(2,3-5.7)	(0-0.1)
	Test	W ₁₀ =95		W ₁₀ =97.5		W ₁₀ =100	
Height (m)	Median	0.3	-	0.3 ^{a***}	0 ^{b***}	0.3 ^{a***}	0.1 ^{b***}
	Min-Max	(0-0.6)	-	(0.1-0.6)	(0-0.1)	(0.2-0.5)	(0-0.2)
	Test	-		W ₁₀ =98.5		W ₁₀ =99	

***(P<0.001)

Long effects of solarization on invasive species

As time passed, the short-term effects of solarization on invasive species ceased. From the second sampling phase on, no differences were found between solarized and unsolarized plots in percentage cover, cover repetition, or height of Nutgrass (F_{1,10}=1.03, P>0.05; F_{1,10}=1.14, P>0.05; F_{1,10}=1.45, P>0.05, respectively) and African Liverseed Grass (F_{1,10}= 0.68, P>0.05; F_{1,10}= 5.22, P>0.05; F_{1,10}= 0.13, P>0.05, respectively).

Seed rain

A total of 77,456 seeds (3,873seeds/m²/year) in 78 morpho species were collected (Appendix 3). Considering zoochoric dispersal only, the collectors beneath the perches accumulated higher seed numbers (n=4,143; median=138.5; min-max=8.0-1,014.0) than collectors in open field (n= 1,356; median=31; min-max=0.0-351.0) ($W_{20}= 312$, $P<0.01$). The species accumulation curve also indicated higher richness of zoochoric seed beneath artificial perches than in open field (Fig.2).

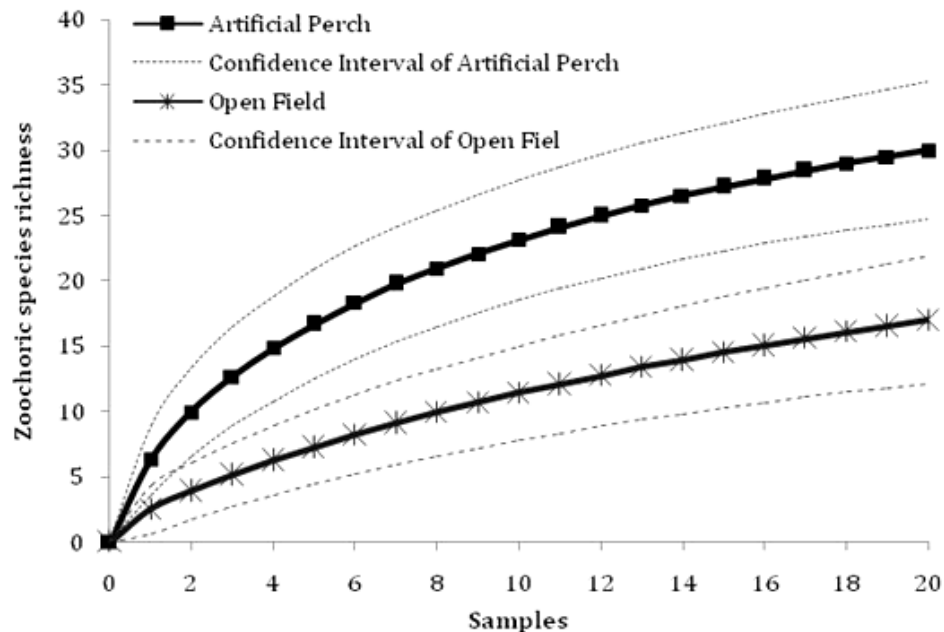


Fig.2. Species accumulation curve (Mao Tau) for zoochoric seeds collected beneath artificial perches and in open field.

Effects of the combined use of artificial perches and solarization on plant community

We found a total of 34 plant community species (Appendix 4) in all the sampling phases and treatments. Only the solarization treatment influenced the accumulated number of species per plot ($F_{1,10}= 7.76$; $P<0.05$). More species were found in unsolarized than in solarized plots (Fig.3A). The artificial perch treatment ($F_{1,10}= 0.13$; $P>0.05$) and the combination of both treatments ($F_{1,10}= 0.03$; $P>0.05$) did not affect the number of accumulated species per plot (Fig.3A). The species accumulation curves suggest equality in species richness among all combinations of treatments applied (Fig. 3B).

The IndVal Test identified seven species with specificity and fidelity in the solarization treatment, but no specificity for species in the artificial perch treatment. In unsolarized plots, the species Velvetleaf (*Cissampelos pareira*, 77.4%; $P<0.01$), Wild Pea (*Vigna adenantha*, 69.9%; $P<0.01$), Florida Key Morning-glory (*Ipomoea tiliacea*, 63.9%; $P<0.05$), Willdenow's Maiden Fern (*Thelypteris interrupta*, 61.8%; $P<0.05$), *Vernonia scorpioides* (39.4%; $P<0.01$), *Eupatorium tubaraoense* (38.5%; $P<0.01$), and Spadeleaf (*Centella asiatica*, 33.5%; $P<0.05$) also presented specificity and fidelity.

The ANOVA of split plots corroborated the effect of solarization on plant community species establishment, as species cover repetition ($F_{1,10}= 9.69$; $P<0.01$) and height ($F_{1,10}= 16.92$; $P<0.01$) were lower in solarized plots than in unsolarized plots (Fig. 4). No differences were found in species percentage cover for the solarization treatment ($F_{1,10}= 4.05$; $P>0.05$). The artificial perch treatment had no effect on species percentage cover ($F_{1,10}=$

0.14; $P > 0.05$), cover repetition ($F_{1,10} = 1.25$; $P > 0.05$), or height ($F_{1,10} = 3.56$; $P > 0.05$) (Fig. 4). No significant interaction was found between solarized and artificial perch treatments on percentage cover ($F_{1,10} = 0.30$; $P > 0.05$), cover repetition ($F_{1,10} = 0.87$; $P > 0.05$), or height ($F_{1,10} = 0.12$; $P > 0.05$) for these species (Fig. 4).

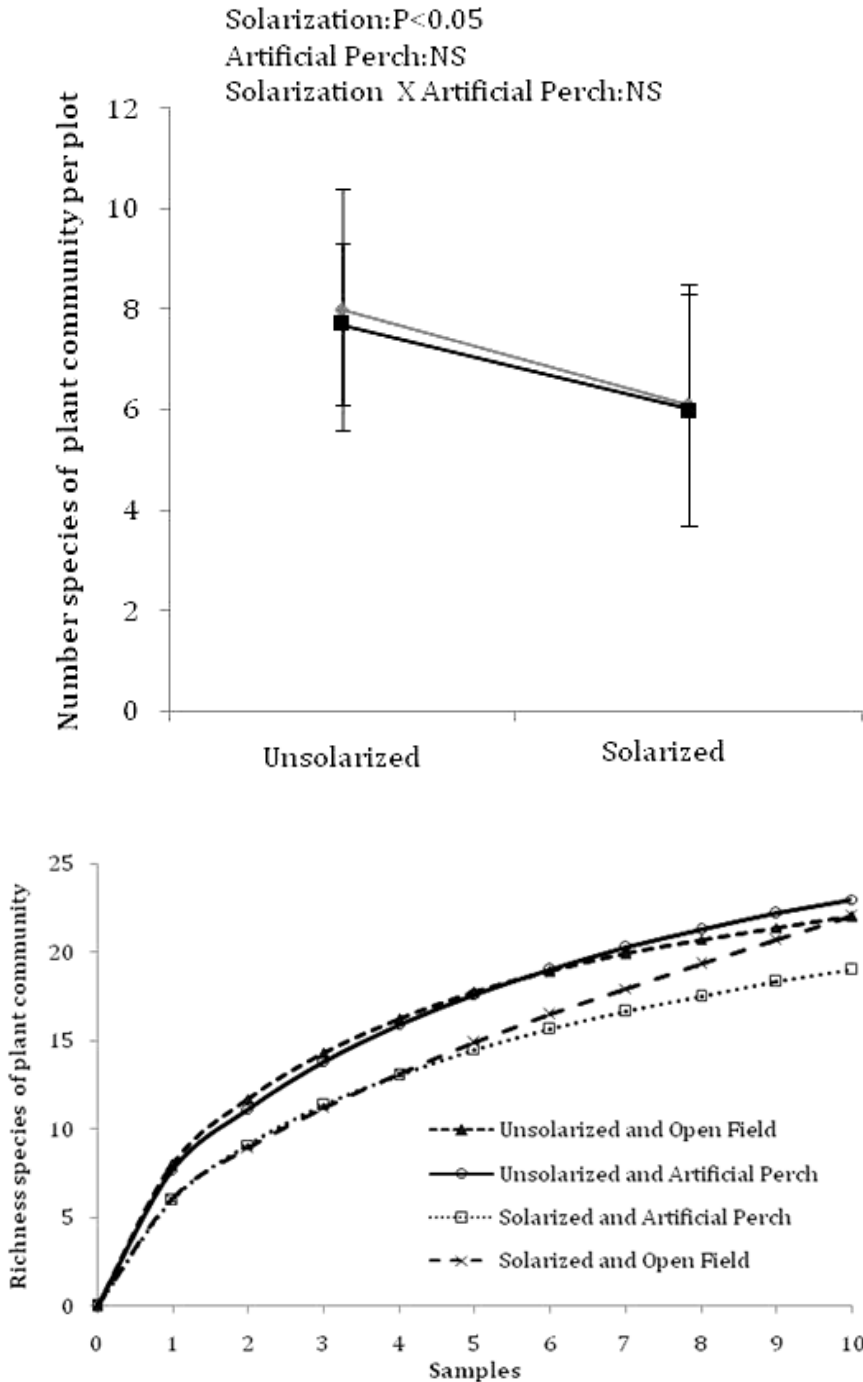


Fig.3. (A) Accumulated number of species of plant community per plot (1 m²) per year, and (B) Plant community species accumulation curve (Mao Tau). In (A), darker line = Artificial perch, and lighter line = Open field; bars represent the average, vertical lines represent the standard deviation around the average. In (B) Confidence Interval for unsolarized and open field = 18.4-25.6; Confidence Interval for unsolarized and artificial perch = 19.0-27.2; Confidence Interval for solarized and open field = 14.7-29.3; Confidence Interval for solarized and artificial perch = 14.9-23.1.

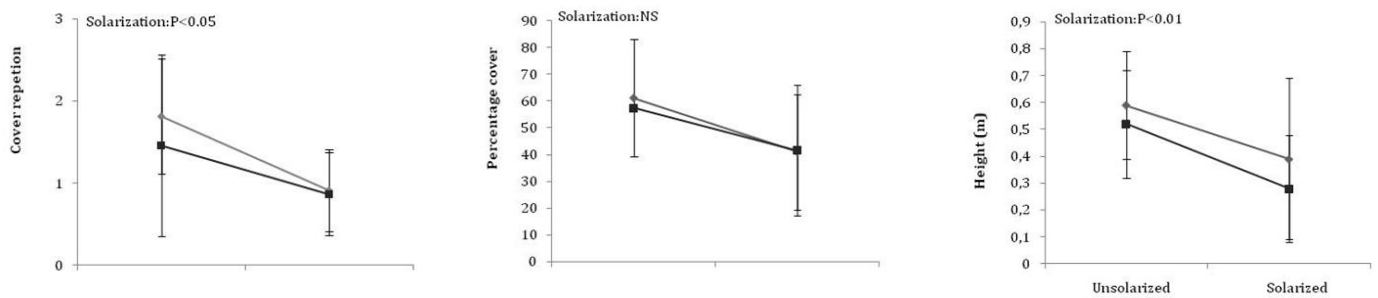


Fig. 4. Average of descriptive variables for regenerating species one year after removal of solarization polyethylene cover, where: darker line = Artificial perch, and lighter line = Open field. The bars represent the standard deviation around the average. The effect significance of each treatment and the interaction between them were tested by ANOVA of split plots. The artificial perch treatment and the interaction between the solarization and artificial perch treatments, for every descriptive variable, are not significant.

Discussion

Due to the rapid regrowth of invasive species in the solarized plots, the combined use of solarization and artificial perches in this study did not result in increased establishment of plant community species within one year of monitoring.

Solarization initially eliminated the invasive species Nutgrass and African Liverseed Grass. This result corroborates the efficacy of the solarization technique in restoration of other environments where it is more commonly used as a pre-treatment for areas densely invaded by non-native or invasive species [26]. All other local plant community species, however, were also eliminated by solarization.

No difference was found in percentage cover, cover repetition, or height for the invasive species three months after removal of the polyethylene cover in solarized and unsolarized plots. We observed that Nutgrass and African Liverseed Grass propagated vegetatively from the borders of solarized plots, where vegetative structures were not covered, as was also observed by Elmore et al. [30] using solarization in prairie habitat. Wilson et al. [24] and Pfeifer-Meister et al. [28] also found that solarization had short-lasting effects in prairie habitat due to the fast regrowth of pest plants and non-native species, respectively. On the other hand, and contrary to these studies, Marushia & Allen [14] found the effects of solarization on non-native grassland in prairie habitat to last during two years of monitoring. Grose [27] found satisfactory and lasting results on non-native species using solarization to restore an area of original forest habitat, although control of non-native species with a specific non-residual herbicide along unsolarized plot borders became necessary. To achieve lasting benefits from the solarization treatment, we recommend periodic management of invasive species around solarized areas.

Artificial perches increased abundance and richness of zoochoric seeds, corroborating studies showing that such structures are efficient in attracting seed dispersers to degraded areas [6-7]. Only two zoochoric species, Seasonvine (*Cissus verticillata*) and Creeping Cucumber (*Melothria pendula*), however, established beneath artificial perches. Both species are climbers and therefore compete with our focal invasive species Nutgrass and African Liverseed Grass by growing over them. Although other zoochoric species were recorded in the plant community, they resprouted from previously established plants after the initial trimming operation, and low recruitment indexes of zoochoric species were therefore found beneath artificial perches, as also noted by Holl et al. [3], Graham & Page [10], and Shiels & Walker [11]. The seed dispersed beneath artificial perches, however, may be restoring the local seed bank [5].

The growth of the invasive species Nutgrass and African Liverseed Grass was very aggressive in both solarized and unsolarized plots. Both species are vigorous reproducers, especially by vegetative means [34-35]. The combination of distinct vegetative propagation techniques (underground, in the case of Nutgrass, and aerial, in the case of African Liverseed Grass) may have increased their competitive edge over other species, inhibiting recruitment and limiting plant community biodiversity [46]. Solarization decreased establishment, height, and cover repetition of some plant community species, contrary to findings by Hooper et al. [13] and by Wilson et al. [24]. These negative effects may have occurred because solarization is not selective, depleting or inhibiting the entire seed bank for both target and non-target species wherever applied [23]. Also, many species have seeds induced in secondary dormancy by the high temperatures during solarization [47] or due to anoxia and/or photoinhibition, the latter induced by the use of black polyethylene [14].

Our study indicates that solarization is efficient in controlling invasive species in the short term, and that artificial perches increase the influx of zoochoric seeds to degraded areas. We observed that the combined use of solarization and artificial perches was limited by the inability of seeds to germinate and establish due to competition from faster-growing invasive species. These rapidly propagated vegetatively from untreated areas into solarized areas. For similar forest restoration work, we suggest additional management of invasive species on the edges of plots, after solarization, to extend its initial effects on the control of invasive species.

Implications for conservation

Solarization with black polyethylene proved to be efficient in eliminating the invasive species Nutgrass and African Liverseed Grass in the short term in a subtropical environment.

Artificial perches proved to be efficient in attracting seed dispersal agents to the degraded area and may enable restoration of the local seed bank.

The solarization should be applied with periodic management of its borders for continuity of its short effects, allowing the recruitment of the desired species.

Acknowledgements

We are grateful to the National Scientific and Technological Development Council (Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq) for a master's degree scholarship to the first author, which made our research work viable, and to Márcia C. M. Marques, Nivaldo Peroni, Rafael Trevisan, Silvia R. Ziller, Luiz R. Zamith and anonymous reviewers for their revisions and invaluable comments to improve this paper.

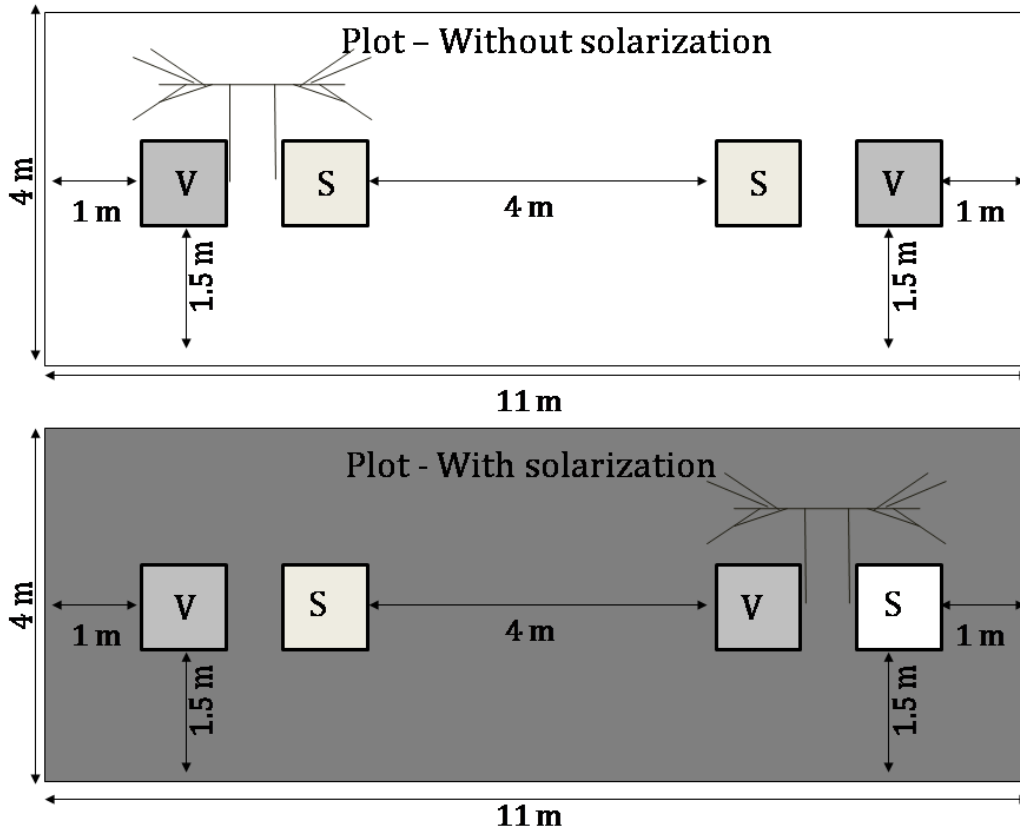
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Appendix 1. Experimental outline scheme using factorial combination in split plots for solarization treatment (full plot factor) – with and without solarization, and artificial perch treatment (subplot factor) – with and without artificial perch (open field). V= permanent vegetation monitoring plot and S = seed collector.



Appendix 2. Formulas used to calculate percentage cover, cover repetition, and average height for the invasive species Nutgrass (*Cyperus rotundus*) and African Liverseed Grass (*Urochloa arrecta*) and plant community species.

PC_i=100 (O_i/P), where:

PC_i = percentage cover for species i;

O_i = total number of points where species i occurs;

P= total number of sampled points in plot = 25 points.

RC_i= C_i/P, where:

RC_i= cover repetition for species i;

C_i= total number of contacts of species i;

P= number of sampled points in plot = 25 points.

A_i=(∑C_{ai} H_{ji})/C_i, where:

A_i = average height of species i;

C_{ai} = number of contacts of species i in height class j;

H_{ji} = average value of height class j (classes: 1=0.13; 2=0.38; 3=0.76; 4=1.13; 5=1.38; 6=1.63; 7=1.88; 8=2.25 m)

C_i= total number of contacts intercepted by species i in the plot.

Appendix 3. List of species with vernacular names (where # represents the ones also found in local vegetation) found in seed rain beneath artificial perches and in open field with respective numbers of seeds /m²/year, dispersal syndrome, life form and origin, where * indicates invasive non-native species.

Family	Species	Nº seeds / m ² /year		Dispersal syndrome	Life form	Origin
		Artificial perch	Open field			
Acanthaceae	<i>Hygrophila brasiliensis</i> (Spreng.) Lindau# n.a.	26.7	2.2	Autochoric	Herb	Native
Anarcadiaceae	<i>Schinus terebinthifolia</i> Raddi Brazilian Peppertree	0.1	0.0	Zoochoric	Tree	Native
Apocynaceae	<i>Forsteronia pubescens</i> A. DC. n.a.	0.0	0.2	Anemochoric	Liana	Native
Arecaceae	<i>Archontophoenix</i> sp. King Palm	0.5	0.0	Zoochoric	Palm	Non-native*
	<i>Euterpe edulis</i> Mart. Jicara	0.1	0.0	Zoochoric	Palm	Native
Asteraceae	Asteraceae 1	0.0	0.1	Anemochoric	Not identified	Not identified
	Asteraceae 2	0.1	0.0	Anemochoric	Not identified	Not identified
	Asteraceae 3	0.1	0.0	Anemochoric	Not identified	Not identified
	Asteraceae 4	1.2	0.6	Anemochoric	Not identified	Not identified
	Asteraceae 5	0.8	1.7	Anemochoric	Not identified	Not identified
	<i>Ageratum conyzoides</i> L. Floss Flower	0.0	0.0	Anemochoric	Subshrub	Native
	<i>Baccharis trinervis</i> Pers.# n.a.	43.4	47.4	Anemochoric	Liana	Native

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Family	Species	N° seeds / m ² /year		Dispersal syndrome	Life form	Origin	
		Artificial perch	Open field				
Asteraceae	<i>Erigeron</i> sp. n.a.	0.0	2.2	Anemochoric	Not identified	Non-native	
	<i>Eupatorium tubaraoense</i> Hieron.# n.a.	9.3	55.7	Anemochoric	Subshrub	Native	
	<i>Hypochaeris</i> sp. n.a.	0.1	0.3	Anemochoric	Herb	Native	
	<i>Mikania campanulata</i> Gardner# n.a.	111.7	130.2	Anemochoric	Liana	Native	
	<i>Piptocarpha tomentosa</i> Baker n.a.	2.8	2.8	Anemochoric	Tree	Native	
	<i>Vernonia scorpioides</i> (Lam.) Pers.# n.a.	4.5	3.7	Anemochoric	Subshrub	Native	
	<i>Vernonia tweediana</i> Baker n.a.	9.0	5.0	Anemochoric	Shrub	Native	
	Boraginaceae	<i>Cordia monosperma</i> (Jacq.) Roem. & Schult.# Black-sage	0.8	1.0	Zoochoric	Shrub	Native
		Bromeliaceae					
	<i>Tillandsia</i> sp. Aerophytes	0.3	0.6	Anemochoric	Herb	Native	
Cactaceae	Cactaceae 1	31.0	0.0	Zoochoric	Not identified	Not identified	
	Cactaceae 2	15.7	0.1	Zoochoric	Not identified	Not identified	
Cannabaceae	<i>Trema micrantha</i> (L.) Blume Jamaican Nettle tree	1.8	0.3	Zoochoric	Tree	Native	
	Caryophyllaceae						
	<i>Drymaria cordata</i> (L.) Willd. ex Roem. & Schult. West Indian Drymary	0.2	0.0	Zoochoric	Herb	Native	
Clethraceae	<i>Clethra scabra</i> Pers. n.a.	0.4	0.4	Anemochoric	Tree	Native	

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Family	Species	Nº seeds / m ² /year		Dispersal syndrome	Life form	Origin
		Artificial perch	Open field			
Clusiaceae	<i>Clusia criuva</i> Cambess. n.a.	0.0	0.2	Zoochoric	Tree	Native
Cyperaceae	<i>Cyperus rotundus</i> L.# Nutgrass	718.1	299.8	Autochoric	Herb	Non-native*
	<i>Cyperus</i> sp. Flatsedge	0.8	0.5	Autochoric	Not identified	Not identified
	<i>Fuirena robusta</i> Kunth n.a.	0.8	0.0	Autochoric	Herb	Native
	<i>Scleria</i> sp. Nutrush	1.2	0.0	Zoochoric	Not identified	Native
Euphorbiaceae	<i>Alchornea glandulosa</i> Poepp. n.a.	2.3	0.2	Zoochoric	Tree	Native
	Euphorbiaceae 1	0.1	0.0	Not identified	Not identified	Not identified
Fabaceae	Fabaceae 1	0.3	0.0	Autochoric	Not identified	Not identified
	<i>Mimosa bimucronata</i> (DC.) Kuntze# n.a.	8.1	36.9	Autochoric	Tree	Native
Lauraceae	<i>Cinnamomum zeylanicum</i> Blume Cinnamon	0.5	0.1	Zoochoric	Tree	Non-native
Loranthaceae	Loranthaceae 1 Showy Mistletoe Family	0.1	0.0	Zoochoric	Not identified	Native
Melastomataceae	<i>Leandra australis</i> (Cham.) Cogn. n.a.	217.1	114.3	Zoochoric	Shrub	Native
	<i>Leandra</i> sp. n.a.	19.7	5.7	Zoochoric	Shrub	Native
	<i>Miconia</i> sp. Johnnyberry	42.3	0.0	Zoochoric	Not identified	Native

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Family	Species	N° seeds / m ² /year		Dispersal syndrome	Life form	Origin
		Artificial perch	Open field			
Melastomataceae	<i>Tibouchina cerastifolia</i> Cogn n.a.	235.8	358.0	Autochoric	Shrub	Native
	<i>Tibouchina urvilleana</i> (DC.) Cogn.# Princessflower	1.0	28.2	Autochoric	Shrub	Native
Mirtaceae	<i>Eugenia</i> sp. n.a.	1.0	0.1	Zoochoric	Not identified	Native
	<i>Myrcia</i> sp. n.a.	0.2	0.0	Zoochoric	Not identified	Native
	Myrtaceae 1	0.1	0.0	Zoochoric	Not identified	Native
Moraceae	<i>Ficus</i> sp. Figs	1.2	0.7	Zoochoric	Tree	Native
Onagraceae	<i>Ludwigia longifolia</i> (DC.) H. Hara# Longleaf Primrose-willow	1,524.8	2,836.9	Autochoric	Subshrub	Native
	<i>Ludwigia octovalvis</i> (Jacq.) P.H. Raven# Shrubby Ludwigia	127.6	2.5	Autochoric	Subshrub	Native
Piperaceae	<i>Piper</i> sp. Pepper	17.4	0.0	Zoochoric	Not identified	Native
Poaceae	<i>Andropogon leucostachyus</i> Kunth n.a.	2.6	2.0	Anemochoric	Herb	Native
	<i>Urochloa arrecta</i> (Hack. ex T. Durand & Schinz) Stent# African Liverseed Grass	172.0	346.0	Autochoric	Herb	Non-native*
	<i>Cenchrus</i> sp. n.a.	0.0	0.1	Zoochoric	Not identified	Native
	<i>Digitaria</i> sp. n.a.	1.0	0.1	Anemochoric	Herb	Not identified

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Family	Species	Nº seeds / m ² /year		Dispersal syndrome	Life form	Origin
		Artificial perch	Open field			
Poaceae	<i>Panicum polygonatum</i> Schrad.# Bolivian Panicgrass	13.1	2.7	Autochoric	Herb	Native
	<i>Paspalum</i> sp. n.a.	0.2	0.0	Autochoric	Herb	Native
	Poaceae1	0.3	0.0	Not identified	Not identified	Not identified
	Poaceae2	0.2	0.0	Not identified	Not identified	Not identified
	Poaceae3	0.0	0.1	Not identified	Not identified	Not identified
	Poaceae4	0.0	0.1	Anemochoric	Not identified	Not identified
Primulaceae	<i>Myrsine coriacea</i> (Sw.) R. Br. ex Roem. & Schult. Leathery Colicwood	5.5	3.4	Zoochoric	Tree	Native
Rosaceae	<i>Rubus brasiliensis</i> Mart. n.a.	0.6	0.3	Zoochoric	Subshrub	Native
Rubiaceae	<i>Psychotria</i> sp.1 n.a.	0.3	0.0	Zoochoric	Not identified	Native
	<i>Psychotria</i> sp.2 n.a.	1.4	0.0	Zoochoric	Not identified	Native
Solanaceae	<i>Solanum americanum</i> Mill. American Black Nightshade	3.3	3.0	Zoochoric	Herb	Native
Typhaceae	<i>Typha</i> sp. n.a.	0.6	0.2	Anemochoric	Herb	Native
Urticaceae	<i>Cecropia glaziovii</i> Snethl. n.a.	27.7	4.7	Zoochoric	Tree	Native
Verbenaceae	<i>Citharexylum myrianthum</i> Cham. n.a.	0.4	0.0	Zoochoric	Tree	Native

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Family	Species	N° seeds / m ² /year		Dispersal syndrome	Life form	Origin
		Artificial perch	Open field			
Vitaceae	<i>Cissus verticillata</i> (L.) Nicolson & C.E. Jarvis# Seasonvine	21.7	1.4	Zoochoric	Liana	Native
Zingiberaceae	<i>Hedychium coronarium</i> J. Koenig White Garland-lily	0.1	0.0	Zoochoric	Herb	Non-native*
Not identified	NI1	1.1	0.9	Not identified	Not identified	Not identified
	NI2	0.0	0.2	Not identified	Not identified	Not identified
	NI3	0.1	0.0	Not identified	Not identified	Not identified
	NI4	0.0	0.1	Not identified	Not identified	Not identified
	NI5	0.1	0.0	Not identified	Not identified	Not identified
	NI6	0.1	0.0	Not identified	Not identified	Not identified
	NI7	0.1	0.0	Not identified	Not identified	Not identified
	NI8	0.9	0.0	Not identified	Not identified	Not identified
	NI9	4.9	0.0	Not identified	Not identified	Not identified
Total		3,439.4	4,303.9			

Appendix 4. List of invasive species and species of plant community with vernacular names registered with respective average percentage cover recorded in the five sampling phases for each combination of treatments. Sol - = unsolarized, Sol + = solarized; dispersal syndrome; life form, origin; # represents species also found in seed rain beneath artificial perches and in open field and * indicates invasive non-native species.

Family	Species	Percentage cover (%)				Dispersal syndrome	Life form	Origin
		Sol - Open field	Sol - Artificial perch	Sol + Open field	Sol + Artificial perch			
Acanthaceae	<i>Hygrophila brasiliensis</i> (Spreng.) Lindau# n.a.	0.00	0.00	4.56	2.08	Autochoric	Herb	Native
Apiaceae	<i>Centella asiatica</i> (L.) Urb. Spadeleaf	1.28	0.48	0.08	0.00	Autochoric	Herb	Non-native*
Apocynaceae	<i>Oxypetalum wightianum</i> Hook. & Arn. n.a.	0.00	0.16	0.00	0.16	Anemochoric	Liana	Native
Asteraceae	<i>Baccharis trinervis</i> Pers.# n.a.	2.16	0.56	0.08	0.00	Anemochoric	Liana	Native
	<i>Eupatorium tubaraoense</i> Hieron.# n.a.	5.68	2.24	0.16	0.16	Anemochoric	Subshrub	Native
	<i>Mikania campanulata</i> Gardner # n.a.	0.08	0.00	0.00	0.00	Anemochoric	Liana	Native
	<i>Mikania cordifolia</i> (L. f.) Willd. Florida Keys Hempvine	0.32	0.16	0.72	0.08	Anemochoric	Liana	Native
	<i>Mikania ulei</i> Hieron. n.a.	0.00	0.00	0.08	0.00	Anemochoric	Liana	Native
	<i>Vernonia scorpioides</i> (Lam.) Pers.# n.a.	5.60	5.28	0.16	0.00	Anemochoric	Subshrub	Native

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Family	Species	Percentage cover (%)				Dispersal syndrome	Life form	Origin
		Sol - Open field	Sol - Artificial perch	Sol + Open field	Sol + Artificial perch			
Asteraceae	<i>Wedelia paludosa</i> DC. n.a.	0.00	0.00	0.32	0.00	Autochoric	Herb	Native
Bignoniaceae	<i>Clytostoma sciuripabulum</i> (K. Schum.) Bureau & K. Schum. n.a.	0.16	0.40	0.00	0.00	Anemochoric	Liana	Non-native
Blechnaceae	<i>Blechnum serrulatum</i> Rich. Swamp Fern	2.32	3.28	6.72	4.32	---	Herb	Native
Boraginaceae	<i>Cordia monosperma</i> (Jacq.) Roem. & Schult.# Black-sage	2.16	0.64	0.00	0.00	Zoochoric	Shrub	Native
Commelinaceae	<i>Commelina diffusa</i> Burm. f. Climbing Dayflower	1.44	1.12	1.36	2.56	Autochoric	Herb	Native
Convolvulaceae	<i>Ipomoea tiliacea</i> (Willd.) Choisy Florida Key Morning-glory	9.60	4.88	2.48	4.56	Autochoric	Liana	Native
Cucurbitaceae	<i>Melothria pendula</i> L. Creeping Cucumber	0.08	0.08	0.24	1.44	Zoochoric	Liana	Native
Cyperaceae	<i>Cyperus rotundus</i> L.# Nutgrass	66.64	48.48	33.76	38.08	Autochoric	Herb	Non-native*
	<i>Kyllinga pumila</i> Michx. Low Spikesedge	0.00	0.00	0.08	0.00	Autochoric	Herb	Native
	<i>Rhynchospora asperula</i> (Nees) Steud. n.a.	0.00	0.00	0.32	0.24	Autochoric	Herb	Native
Euphorbiaceae	<i>Alchornea triplinervia</i> (Spreng.) Müll. Arg. n.a.	0.00	0.40	0.00	0.00	Zoochoric	Tree	Native
Fabaceae	<i>Desmodium adscendens</i> (Sw.) DC. Zarabacoa Galana	1.68	0.00	0.00	0.24	Zoochoric	Subshrub	Native

CONTINUED

Family	Species	Percentage cover (%)				Dispersal syndrome	Life form	Origin
		Sol - Open field	Sol - Artificial perch	Sol + Open field	Sol + Artificial perch			
Fabaceae	<i>Mimosa bimucronata</i> (DC.) Kuntze# n.a.	1.20	0.32	0.08	0.00	Autochoric	Tree	Native
	<i>Vigna adenantha</i> (G. Mey.) Maréchal. Mascherpa & Stainier Wild Pea	14.40	11.60	5.76	5.44	Autochoric	Liana	Native
Lygodiaceae	<i>Lygodium volubile</i> Sw. n.a.	0.00	2.40	0.00	0.00	---	Liana	Native
Melastomataceae	<i>Tibouchina urvilleana</i> (DC.) Cogn.# Princessflower	4.64	5.36	0.00	0.00	Autochoric	Shrub	Native
Menispermaceae	<i>Cissampelos pareira</i> L. Velvetleaf	8.08	8.24	1.12	0.48	Autochoric	Liana	Native
Onagraceae	<i>Ludwigia longifolia</i> (DC.) H. Hara# Longleaf Primrose-willow	0.24	0.08	0.80	0.88	Autochoric	Subshrub	Native
	<i>Ludwigia octovalvis</i> (Jacq.) P.H. Raven# Shrubby Ludwigia	0.00	0.00	0.00	2.40	Autochoric	Subshrub	Native
Poaceae	<i>Urochloa arrecta</i> (Hack. ex T. Durand & Schinz) Stent# African Liverseed Grass	42.88	64.88	55.76	52.08	Autochoric	Herb	Non- native*
	<i>Ischaemum minus</i> J. Presl n.a.	2.32	4.48	0.48	1.60	Autochoric	Herb	Native
	<i>Panicum polygonatum</i> Schrad.# Bolivian Panicgrass	3.52	0.16	0.00	0.72	Autochoric	Herb	Native
	<i>Panicum schwackeanum</i> Mez n.a.	0.08	0.72	0.56	0.48	Autochoric	Herb	Native

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Family	Species	Percentage cover (%)				Dispersal syndrome	Life form	Origin
		Sol - Open field	Sol - Artificial perch	Sol + Open field	Sol + Artificial perch			
Thelypteridaceae	<i>Thelypteris interrupta</i> (Willd.) K. Iwats. Willdenow's Maiden Fern	30.00	25.04	14.72	14.80	---	Herb	Native
Vitaceae	<i>Cissus verticillata</i> (L.) Nicolson & C.E. Jarvis# Seasonvine	0.00	0.00	0.08	0.56	Zoochoric	Liana	Native