

“Cerrado” restoration by direct seeding: field establishment and initial growth of 75 trees, shrubs and grass species

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Abstract The coexistence of grasses, herbs, shrubs and trees characterizes savannas; therefore, to restore such ecosystems one should consider re-introducing all these growth forms. Currently, little is known about field establishment of most “Cerrado” (Brazilian savanna) species that could be used for restoration purposes. Most knowledge on restoration is focused on planting seedlings of tree species from forest physiognomies. Alternatively, direct seeding can be an appropriate method to re-introduce plants of different life forms to restore savannas. We evaluated the initial establishment success under field conditions of 75 “Cerrado” native species (50 trees, 13 shrubs, and 12 grasses) in direct seeding experiments in four sites in Central Brazil for 2.5 years. For that, we tagged and measured tree and larger shrub species and estimated ground cover by small shrub and grass species.

Sixty-two species became established (42 trees, 11 shrubs and 9 grasses) under field conditions. Thirty-eight of the 48 tagged species had relatively high emergence rates (>10%) and 41 had high seedling survival (>60%) in the first year. Among grasses and small shrub species, *Andropogon fastigiatus* Sw., *Aristida riparia* Trin., *Schizachyrium sanguineum* (Retz.) Alston, *Lepidaploa aurea* (Mart. ex DC.) H. Rob., *Stylosanthes capitata* Vogel, *S. macrocephala* M.B. Ferreira & Sousa Costa, *Achyrocline satureioides* (Lam.) DC. and *Trachypogon spicatus* (L.f.) Kuntze had the greatest initial establishment success (up to 30% soil cover). The data on harvesting period, processing mode and field establishment for these 75 species can be readily used in restoration efforts in the “Cerrado”.

Keywords Direct sowing · Ecological restoration · Grassland restoration · Herbaceous layer · Neotropical savanna

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Introduction

Savannas are naturally dominated by an herbaceous layer with tree density varying according to soil and climate conditions and fire regime, among other factors (Higgins et al. 2000). Therefore, ecological restoration of such areas must consider the original vegetation structure in order to actually contribute to conservation of biodiversity and ecosystem services (Chazdon 2008; Veldman et al. 2015a). Nevertheless, because most restoration studies are focused on forest ecosystems, restoration recommendations in both scientific and practical arenas are mostly focused on tree planting (Ruiz-Jaen and Aide 2005; Rodrigues et al. 2009). Afforestation or equivocal restoration threaten savanna and grassland ecosystems by decreasing endemic plant and animal diversity, decreasing ground water recharge and increasing aboveground biomass allocation, which increases susceptibility to fire events (Veldman et al. 2015b).

The dominance of exotic invasive species is a frequent challenge for restoring degraded ecosystems (Durigan et al. 2013; Holl et al. 2014). This is especially true in tropical savannas and grasslands, which are commonly dominated by invasive grasses (Williams and Baruch 2000). Invasive grass species reduce light and water availability (Levine et al. 2003); intensify fire regimes (D'Antonio and Vitousek 1992); and alter other ecosystem features (Chapin et al. 2000). Most grass species are shade-intolerant and can be eliminated by fast-growing forest trees in restoration areas, as long as fire and other disturbances are excluded (Cabin et al. 2002). However, planting fast-growing tree species that could outcompete these invasive grasses might not be possible or appropriate to restore grassland and savanna ecosystems (Veldman et al. 2015b). Besides, the seedlings from most native savanna tree species are slow-growing due to higher investment in below-ground tissues (De Castro and Kauffman 1998), which allows for survival during the dry season. In addition, native herbaceous and shrub species are important parts of open ecosystems structure, function and diversity (Mendonça et al. 2008; Bond and Parr 2010). Therefore, to effectively restore savanna and grassland environments, it is essential to select and use herbaceous and shrub species that can establish and compete with invasive grasses, without excluding slow-growing tree species.

The “Cerrado” phytogeographical domain, in Central Brazil, is a biodiversity hotspot due to its high levels of endemism and high rates of conversion of native vegetation (da Silva and Bates 2002). It is the most biodiverse savanna region in the world, where millions hectares are targeted to be restored by federal legislation (Brasil 2000; Soares Filho et al. 2014). To effectively restore such vast areas, it is urgent to improve knowledge on restoration ecology, and

the first step should be generating information on species propagation and establishment in field conditions. There are more than 12,000 plant species native from the “Cerrado” domain, many of which are endemic, and about 6000 are herbaceous (Ratter et al. 1997; Mendonça et al. 2008). Tree species diversity is high, especially in riparian forests, whereas herbs and shrubs represent 87% of the flora in the grassland and savanna physiognomies (Mendonça et al. 2008), which originally covered around 70% of the “Cerrado” domain (Sano et al. 2007). Native species from “Cerrado” grassland and savanna physiognomies, hereafter referred as “Cerrado”, were rarely tested for field establishment (Silva et al. 2015), and very little is known about the use of herbaceous species for restoration in the Brazilian savanna (see Filgueiras and Fagg 2008; Aires et al. 2014). In the Federal District of Brazil, forest trees are often used to restore areas originally covered by “Cerrado”, due to their faster growth rates, higher seed production and availability on nurseries (de Sousa 2015). This practice is also widespread across savanna ecosystems in the rest of Brazil.

Low-cost and effective methods are desirable for large-scale restoration (Holl and Aide 2011; Campos Filho et al. 2013). Direct seeding is a relatively low-cost restoration technique that allows for the introduction of different plant growth forms simultaneously. While it is commonly applied worldwide in open ecosystems such as grasslands (Palma and Laurance 2015), restoration of savanna ecosystems in Brazil through direct seeding is still rare (Silva et al. 2015) and grassland restoration is almost nonexistent (Overbeck et al. 2013).

In this study, we aimed to investigate the establishment success in field conditions of a large number of species, of different growth forms, that could potentially be used in restoration experiments and practice. We present results of seedling emergence in both greenhouse and field conditions, as well as seedling survival in the field for 75 species (50 tree species, 13 shrubs and 12 grasses) native to “Cerrado” up to 2.5 years after seeding. Our results provide important information for species selection in restoration efforts in “Cerrado” areas.

Methods

Study sites – We evaluated the establishment success of 75 species seeded in seven restoration experiments in four sites in Central Brazil. Three study sites were located in the Federal District: (1) Água Limpa Experimental Farm of University of Brasília (15°56'55"S, 47°56'03"W); (2) Contagem Biological Reserve (15°38'58"S, 47°51'53"W); (3) Entre Rios Farm (15°57'30"S, 47°27'26"W), a private

Table 1 Study sites, experimental and restoration areas through direct seeding of 75 savanna species in Central Brazil

Site	Altitude (m)	Annual rainfall (mm)	Year of seeding	Soil type	Restoration total area (m ²)	Experimental design	Experimental area	Sampled area
1	1080	1460	2011 ^a	Latosol	486	54 × 6 m × 1.2 m beds	389 m ²	389 m ²
2	1100	1668	2012 ^a	Latosol	30,000	36 × 30 m rows	1080 m	1080 m
			2013		29,000	6 × 20 m × 20 m plots	2400 m ²	120 m ²
3	1060	1350	2013	Cambisol	2400	6 × 20 m × 20 m plots	2400 m ²	120 m ²
4	1240	1453	2012 ^a	Latosol	30,000	15 × 10 m × 100 m plots	15,000 m ²	135 m ²
			2013		30,000	12 × 20 m × 20 m plots	4800 m ²	240 m ²
			2014		30,000	18 × 20 m × 20 m plots	7200 m ²	360 m ²

^a We controlled weeds only on areas sown in 2011 and 2012 by manual weeding and/or mechanized mowing between beds, rows and plots

farm. Site 4, Chapada dos Veadeiros National Park (14°07'03"S, 47°38'31"W), is located in the state of Goiás (Table 1).

All study sites were originally “Cerrado” *sensu stricto* areas that were converted to pasture. Only site 2 was used for mechanized agriculture, but it was colonized by exotic pasture grasses after abandonment. The study region is within a tropical savanna climate, with dry winters and rainy summers (Aw Köppen); the mean temperature is 21 °C, and average precipitation is 1500 mm (90% of which is concentrated from October to May; INMET 2009). Mean precipitation in the four study sites is similar (Table 1).

Soils are latosols in sites 1, 2 and 4 and cambisols in site 3. All sites were dominated by invasive grass species (more than 98% soil cover), with very low density of native plants (<1 individual, on average, per 10 m² plot). Agricultural activities in all areas had been terminated before the start of restoration experiments. The most common invasive grasses in study sites are also common invaders throughout Brazil and other tropical areas (Zenni and Ziller 2011): *Urochloa decumbens* (Stapf) R.D. Webster, *Urochloa humidicola* (Rendle) Morrone & Zuloaga, *Urochloa brizantha* (Hochst. ex A. Rich.) R.D. Webster, *Andropogon gayanus* Kunth, *Melinis minutiflora* P. Beauv. and *Hyparhenia rufa* (Nees) Stapf.

Experimental design – Direct seeding experiments were carried out from 2011 to 2014 according to the study sites (detailed in Table 1). We collected seeds/propagules used in the direct seeding experiments from areas around the restoration sites in the 8 months preceding the sowing, according to species phenology. We processed propagules according to each species features (detailed in Table 2). For species with seeds larger than 0.3 cm, we selected and eliminated visually unviable seeds (predated, aborted). We stored seeds in paper bags in fresh (room temperature) and dry conditions until sowing. No pre-treatment to break seed dormancy was applied before seeding, except for *Annona crassiflora* Mart. seeds, which were soaked in a gibberellin acid solution (1 g of GA3, 200 mL of alcohol and 1 L of

water) for 48 h. We also used *Stylosanthes* spp. seeds sold commercially (*S. capitata* and *S. macrocephala*), *Campo Grande* variety.

At all sites, soil was plowed one or two times during the dry season (May–October) prior to seeding to decrease dominance by invasive grasses and soil compaction. We carried out direct seeding manually at the beginning of the rainy season (late October–early December) following three field experiment types: sowing beds (6 × 1.2 m); sowing rows (30 m linear meters); and broadcast sowing in whole plots (20 × 20 m), according to year and experimental site (Table 1). We buried hard, large, round-seeded species (≥0.5 cm diameter) by lightly plowing soil after seeding, whereas flat and smaller seeds were seeded after plowing on the soil surface (Table 2).

In sowing rows and beds, we planted one tree seed every 20 cm (one seed m⁻¹ species⁻¹). In seed-broadcasting plots, we sowed 25–34 tree seeds m⁻² along with a mix of grass and shrub species in high density (4–16 species; seed density varying from 5 to 1100 viable seeds m⁻² species⁻¹; Table 3). We chose this relatively high seed density to maximize the chances of promoting fast ground cover by native species and preventing the reestablishment and dominance of invasive grasses.

Data collection – To characterize seedling emergence during the first rainy season, we sampled experimental areas 3 and 6 months after sowing (which corresponds to the middle and the end of the first rainy season). To evaluate survival of woody species and ground cover of herbaceous species, we sampled the experimental areas every 6 months up to 2.5 years, which corresponds to the end of the second rainy season after seeding.

We tagged all seedlings from the 50 tree species and from eight of the shrub species in planting rows and beds, and measured their height (soil to apical bud) every 6 months. To sample seed-broadcasting experiments, we established two 10 m² (20 × 0.5 m) subplots within each 400 m² experimental plot. We estimated ground cover of native grasses and shrubs sowed by using the line-point intercept method (Herrick et al. 2009), sampling 200 points along a 20-m line

Table 2 Growth form; seed collection time; processing mode (removing pulp device “RPD,” sieve, grass shredder machine “GSM,” manual separation “MS”); field planting mode (buried “B,” or not buried “NB”); mean mass of 100 seeds \pm SD (values without SD were measured only once); number of seeds tested in green house (GH) in each year (Y); mean percentage seedling emergence in greenhouse (GHE) \pm SD (values without SD were tested only once—1 year) of Brazilian savanna native species

Species	Family	Growth form	Seed collection	Processing mode	Planting mode	100 seeds (g)	# Seeds GH: Y1; Y2; Y3	GHE (%)
Grass species								
<i>Andropogon bicornis</i> L.	Poaceae	Herb	May	GSM	NB	0.23	300; 100	5.5 \pm 6.0
<i>Andropogon fastigiatus</i> Sw.	Poaceae	Herb	June	GSM	NB	0.11 \pm 0.01	4000	0.0
<i>Andropogon</i> sp.	Poaceae	Herb	July	GSM	NB	0.02	300; 200	19.0 \pm 25.5
<i>Aristida riparia</i> Trin	Poaceae	Herb	May	GSM	NB	0.12 \pm 0.02	100; 100; 200	10.5 \pm 0.9
<i>Aristida</i> aff. <i>riparia</i> .	Poaceae	Herb	June	GSM	NB	0.15 \pm 0.03	100; 4000	1.5 \pm 2.1
<i>Aristida</i> sp1	Poaceae	Herb	May	GSM	NB	0.15 \pm 0.02	100	35.0
<i>Axonopus aureus</i> P.Beauv.	Poaceae	Herb	May	Sieve	NB	0.06 \pm 0.01	na	na
<i>Axonopus pellitus</i> (Nees ex Trin.) Hitchc. & Chase	Poaceae	Herb	May	GSM	NB	0.012 \pm 0.008 (b)	100	4.0
<i>Echinolaena inflexa</i> (Poir.) Chase	Poaceae	Herb	May	Sieve	NB	0.22 \pm 0.04	100	17.0
<i>Loudetiopsis chrysothrix</i> (Nees) Conert	Poaceae	Herb	June	GSM	NB	0.47 \pm 0.05	4000	13.0
<i>Schizachyrium sanguineum</i> (Retz.) Alston	Poaceae	Herb	June	GSM	NB	0.19 \pm 0.05	100; 4000	3.5 \pm 0.7
<i>Trachypogon spicatus</i> (L.f.) Kuntze	Poaceae	Herb	June	GSM	NB	0.24	100; 4000	2.5 \pm 3.54
Shrub species								
<i>Anacardium humile</i> A. St.-Hil.	Anacardiaceae	Shrub	September–October	MS	B	238.39 \pm 7.60	100; 100	63.0 \pm 43.8
<i>Achyrocline satuireioides</i> (Lam.) DC.	Asteraceae	Shrub	August–September	GSM	NB	0.05 \pm 0.00	100	4.0
<i>Aldama bracteata</i> (Gardner) E.E.Schill. & Panero	Asteraceae	Shrub	April–May	GSM	NB	0.15 \pm 0.04	100; 100	48.3 \pm 27.1
<i>Lepidaploa aurea</i> (Mart. ex DC.) H.Rob.	Asteraceae	Shrub	June–	GSM	NB	0.08 \pm 0.03	100; 100	10.5 \pm 0.7
<i>Vernonanthura phosphorica</i> (Vell.) H.Rob.	Asteraceae	Shrub	August	GSM	NB	0.03 \pm 0.00	100	10.0
<i>Jacaranda ulei</i> Bureau & K.Schum.	Bignoniaceae	Shrub	August	Sieve	NB	2.70 (a)	100	8.0
<i>Zeyheria montana</i> Mart.	Bignoniaceae	Shrub	August	Sieve	NB	6.67	100	7.0
<i>Parinari obtusifolia</i> Hook.f.	Chrysobalanaceae	Shrub	October	RPD	B	206.00	100	0.0

Table 2 continued

Species	Family	Growth form	Seed collection	Processing mode	Planting mode	100 seeds (g)	# Seeds GH: Y1; Y2; Y3	GHE (%)
<i>Bauhinia cf dumosa</i> Benth.	Fabaceae	Shrub	October	Sieve	B	372.00 ± 114.00	100	5.0 ± 4.2
<i>Mimosa clausenii</i> Benth.	Fabaceae	Shrub	September	GSM	B	3.16 ± 0.55	100; 100; 100	22.6 ± 12.4
<i>Mimosa</i> sp.	Fabaceae	Shrub	August	Sieve	B	0.93 ± 0.11	100	0.0
<i>Senna alata</i> (L.) Roxb.	Fabaceae	Shrub	June	Sieve	B	5.50 ± 0.28	100; 100	13.0 ± 9.5
<i>Stylosanthes capitata</i> Vogel + S. <i>macrocephala</i> M.B. Ferreira & Sousa Costa ^a	Fabaceae	Shrub	na	na	NB	0.27 ± 0.01	100; 100	23.3 ± 4.6
Tree species								
<i>Anacardium occidentale</i> L.	Anacardiaceae	Tree	September–October	MS	N	448.43	na	na
<i>Astronium fraxinifolium</i> Schott	Anacardiaceae	Tree	September	Sieve	B	5.66 ± 0.26	100; 100	79.3 ± 20.3
<i>Myracrodruon urundeuva</i> Allemão	Anacardiaceae	Tree	September	Sieve	B	1.94 ± 1.68	100; 100; 100	44.0 ± 49.4
<i>Schinopsis brasiliensis</i> Engl.	Anacardiaceae	Tree	August	Sieve	B	14.72 ± 3.23	100; 100	4.5 ± 4.9
<i>Annona crassiflora</i> Mart.	Annonaceae	Tree	March	RPD	B	64.95 ± 5.95	100; 100; 100	26.0 ± 24.0
<i>Aspidosperma macrocarpon</i> Mart.	Apocynaceae	Tree	September	MS	B	85.71 ± 3.72	100; 100	40.0 ± 32.9
<i>Aspidosperma tomentosum</i> Mart.	Apocynaceae	Tree	September	MS	B	21.6	100	46.0
<i>Hancornia speciosa</i> Gomes	Apocynaceae	Tree	October	RPD	B	23.00 ± 1.00	100	63.0
<i>Schefflera macrocarpa</i> (Cham. & Schltdl.) Frodin.	Araliaceae	Tree	July	Sieve	B	5.88 (e)	100; 100	20.0 ± 24.0
<i>Eremanthus glomerulatus</i> Less.	Asteraceae	Tree	September	Sieve	NB	0.40 ± 0.19	200; 100; 100	32.0 ± 40.9
<i>Cybistax antisyphilitica</i> (Mart.) Mart.	Bignoniaceae	Tree	October	MS	NB	1.99 ± 0.04	200	49.0
<i>Handroanthus ochraceus</i> (Cham.) Mattos	Bignoniaceae	Tree	September–October	Sieve	NB	1.32 ± 0.13	100	93.0
<i>Jacaranda brasiliana</i> (Lam.) Pers.	Bignoniaceae	Tree	August	MS	B	2.73 ± 0.15	100; 100; 100	35.3 ± 29.9
<i>Tabebuia aurea</i> (Silva Manso) Benth. & Hook.f. ex S.Moore	Bignoniaceae	Tree	September–October	Sieve	NB	1.43 (a)	na	na
<i>Tabebuia caraiba</i> (Mart.) Bureau	Bignoniaceae	Tree	October	MS	NB	16.93 ± 0.46	100	39.0
<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	Boraginaceae	Tree	October	Sieve	B	7.67 ± 0.13	100	27.0

Table 2 continued

Species	Family	Growth form	Seed collection	Processing mode	Planting mode	100 seeds (g)	# Seeds GH: Y1; Y2; Y3	GHE (%)
<i>Kielmeyera coriacea</i> Mart. & Zucc.	Calophyllaceae	Tree	August–September	MS	NB	10.85 ± 0.25	100; 100	28.0 ± 24.3
<i>Buchenavia</i> sp.	Combretaceae	Tree	September	Sun-dried	B	95.21 ± 0.61	100	0.0
<i>Buchenavia tomentosa</i> Eichler	Combretaceae	Tree	September	Sun-dried	B	113.12 ± 10.77	100	30.0
<i>Terminalia argentea</i> Mart.	Combretaceae	Tree	September	Sieve	B	24.96 ± 0.37	100	15.0
<i>Terminalia fagifolia</i> Mart.	Combretaceae	Tree	September	Sieve	B	1.82	100	2.0
<i>Davilla elliptica</i> A.St.-Hil.	Dilleniaceae	Tree	August	GSM/sieve	B	3.21	100	0.0
<i>Amburana cearensis</i> (Allemão) A.C.Sm.	Fabaceae	Tree	August	Sieve	B	53.64	100; 100	38.7 ± 26.0
<i>Anadenanthera colubrina</i> (Vell.) Brenan	Fabaceae	Tree	August	Sieve	NB	14.20 ± 1.12	100; 100; 100	73.0 ± 36.0
<i>Bowdichia virgilioides</i> Kunth	Fabaceae	Tree	July	MS	B	2.12 ± 0.02 (c)	na	na
<i>Copaifera langsdorffii</i> Desf.	Fabaceae	Tree	August–October	Sieve	B	100.28 ± 9.64	100; 100; 100	44.6 ± 32.9
<i>Dalbergia miscolobium</i> Benth.	Fabaceae	Tree	September	Sieve	B	17.42 ± 1.51	100	12.0
<i>Dimorphandra mollis</i> Benth.	Fabaceae	Tree	June	GSM/sieve	B	17.62 ± 0.37	100	6.0
<i>Dipteryx alata</i> Vogel	Fabaceae	Tree	September	None	B	2259.06 ± 48.47	100;100	32.5 ± 44.5
<i>Enterolobium contortisiliquum</i> (Vell.) Morong	Fabaceae	Tree	October	GSM/sieve	B	45.31 ± 0.81	100;100	3.7 ± 2.3
<i>Enterolobium gummiferum</i> (Mart.) J.F.Macbr.	Fabaceae	Tree	July–August	GSM	B	51.02	na	na
<i>Hymenaea stigonocarpa</i> Mart. ex Hayne	Fabaceae	Tree	September	GSM/sieve	B	373.07 ± 101.86	100; 100; 100	47.5 ± 2.4
<i>Machaerium opacum</i> Vogel	Fabaceae	Tree	August	Sieve	NB	61.83 ± 38.26	100; 100	3.6 ± 3.1
<i>Plathymenia reticulata</i> Benth.	Fabaceae	Tree	August	Sieve	B	4.50 ± 0.06	100	22.0
<i>Senegalia polyphylla</i> (DC.) Britton & Rose.	Fabaceae	Tree	July–ago	Sieve	B	16.41 ± 2.01	100; 100	55.7 ± 25.5
<i>Stryphnodendron adstringens</i> (Mart.) Coville	Fabaceae	Tree	Ago	GSM/sieve	B	9.40 ± 0.52	100; 200	11.3 ± 9.0
<i>Tachigali vulgaris</i> LF Gomes da Silva & HC Lima	Fabaceae	Tree	September	Sieve	B	22.02 ± 0.50	100; 100	44.5 ± 16.3
<i>Vatairea macrocarpa</i> (Benth.) Ducke	Fabaceae	Tree	September	None	B	142.86 (g)	100; 200	13.0 ± 11.3
<i>Emmotum nitens</i> (Benth.) Miers	Icacinaceae	Tree	November	None	B	142.16 ± 34.66(e)	na	na

Table 2 continued

Species	Family	Growth form	Seed collection	Processing mode	Planting mode	100 seeds (g)	# Seeds GH: Y1; Y2; Y3	GHE (%)
<i>Byrsonima crassifolia</i> (L.) Kunth	Malpighiaceae	Tree	April	RPD	B	0.29 ± 0.01(d)	100; 100	24.7 ± 14.4
<i>Cecropia pachystachya</i> Trécul	Urticaceae	Tree	August–September	MS	NB	0.10 ± 0.03	100	0.02
<i>Eriotheca pubescens</i> (Mart. & Zucc.) Schott & Endl.	Malvaceae	Tree	July	Sieve	B	20.78 ± 0.48	100	33.5 ± 7.8
<i>Guazuma ulmifolia</i> Lam.	Malvaceae	Tree	October	GSM/sieve	B	0.63	100	12.0
<i>Tibouchina candolleana</i> (Mart. ex DC.) Cogn.	Melastomataceae	Tree	September	Sieve	NB	0.11 ± 0.07	200; 100	31.7 ± 39.9
<i>Brosimum gaudichaudii</i> Trécul	Moraceae	Tree	October	MS	B	142.86	na	na
<i>Eugenia dysenterica</i> (Mart.) DC.	Myrtaceae	Tree	October	RPD	B	90.97 ± 40.42	100; 100	8.0 ± 6.9
<i>Alibertia edulis</i> (Rich.) A.Rich.	Rubiaceae	Tree	September–November	Sieve	B	0.89 (a)	100	1.0
<i>Magonia pubescens</i> A. St.-Hil.	Sapindaceae	Tree	August	MS	NB	182.32 ± 55.15	100; 100; 100	62.0 ± 38.0
<i>Solanum lycocarpum</i> A. St.-Hil.	Solanaceae	Tree	July–December	RPD	B	2.78 ± 0.76	100; 100; 100	23.0 ± 20.8
<i>Qualea grandiflora</i> Mart.	Vochysiaceae	Tree	October	Sieve	NB	12.0 ± 4.0 (f)	na	na

(a) Salomão et al. (2003), (b) Carmona et al. (1999), (c) Gonçalves et al. (2008), (d) García-Núñez et al. (2001), (e) Kuhlmann (2012), (f) Kutschenko (2009), (g) Mori et al. (2012)

na not available. Species are grouped by life form, listed in alphabetical order by family and species name

^a *Campo Grande* variety, set of these two species sold commercially, evaluated as a sample

in each 10 m² subplot (one point every 10 cm, 200 points per subplot) every 6 months. We placed a 2-m-high stick straight up from the soil at each point and recorded the species touching the stick at the highest height; points with no plant species were recorded as bare soil.

Data analyses – We calculated seedling emergence percentage for 50 trees and eight of the shrub species by comparing the number of seedlings that emerged in the first rainy season (May–June) to the number of sowed seeds. We calculated the survival rates for the first year by comparing the number of plants surviving 12 months after sowing to the number of seedlings that emerged. We calculated the survival rate for the second year by comparing the number of plants still alive after 24 months to the number that survived the first year.

To verify the germinability of seeds used in field experiments, we also sowed seeds in a greenhouse simultaneously to each of the field experiments, except for the 2011 experiment. We distributed seeds of each species in plastic trays filled with subsoil lightly covering the seeds and irrigated daily. We monitored seedling emergence weekly for 16 weeks. For non-grass species, we planted 100 seeds species⁻¹, except for species with low seed numbers. For grass species, we planted 4000 diaspores species⁻¹, due to small seed size and low germinability of native grasses (Table 1).

We tested a different group of species in each experiment; there was seeding density variation across experiments due to variations in site, year and seed availability. We do not intend to compare experiments, sowing methods

Table 3 Grass and shrub species used in savanna direct seeding restoration experiments in three sites in Central Brazil

Species	Sowing density (g m ⁻²)	Soil cover after first rainy season	Soil cover after second rainy season
<i>Achyrocline satureioides</i>	0.880	0.28 ± 0.37	2.12 ± 2.88
<i>Aldama bracteata</i>	0.033	0.12 ± 0.18	0.16 ± 0.19
<i>Andropogon bicornis</i>	0.005	1.43 ± 1.02	0.04 ± 0.38
<i>Andropogon fastigiatus</i>	0.500	30.24 ± 3.79	na
<i>Aristida riparia</i> ^{a,b}	0.100	1.21 ± 1.21	2.19 ± 4.53
<i>Aristida riparia</i> ^a	2.000	2.14 ± 3.10	15.06 ± 12.08
<i>Axonopus aureus</i>	0.080	1.03 ± 1.21	0.47 ± 1.41
<i>Axonopus cf. pellitus</i>	0.002	0.00 ± 0.00	na
<i>Echinolaena inflexa</i>	0.100	0.75 ± 0.67	0.17 ± 0.93
<i>Lepidaploa aurea</i> ^a	0.900	7.43 ± 9.00	6.27 ± 9.98
<i>Lepidaploa aurea</i> ^a	1.125	6.30 ± 4.47	21.25 ± 11.93
<i>Loudetiopsis chrysothrix</i>	0.325	0.74 ± 0.56	0.20 ± 1.82
<i>Schizachyrium sanguineum</i>	0.010	6.89 ± 7.73	15.95 ± 18.47
<i>Stylosanthes</i> spp. ^a	0.060	2.80 ± 3.10	1.93 ± 4.23
<i>Stylosanthes</i> spp. ^a	0.173	4.07 ± 3.16	3.77 ± 3.07
<i>Trachypogon spicatus</i>	0.875	1.48 ± 1.71	2.28 ± 6.86
<i>Vernonanthura phosphorica</i>	0.500	0.18 ± 0.19	na

Sowing density (mean weight of seeds/m² ± SD); soil cover (Mean ± SD) after first and second rainy season

na not available

^a Species represented in more than one line were seeded in more than one experiment; each line represents the sowing density and consequent soil cover of each experiment

^b *Aristida* sp. and *Aristida* aff. *riparia* were also seeded but had low rates of establishment, no flowering in the experimental areas and are not distinguishable from *Aristida riparia* in early stages, so data from these species establishment are not presented here

or even study years; therefore, no comparisons are presented for such purposes. The central aim of the analyses presented here is to synthesize information on seed harvesting period, processing and field establishment success of the studied species.

Results

In field conditions, 62 species (42 trees, 11 shrubs and 9 grasses) produced seedlings in the first rainy season after planting. Of these, 38 (32 trees and six shrubs) had at least 10% emergence in the first rainy season, with 30 of them (27 trees and three shrubs) reaching at least 20%. After the first year, 36 trees and five shrubs had above 60% of survival with 19 of them (17 trees and two shrubs) having emergence above 20 and >80% survival rate. *Anacardium humile*, *Enterolobium gummiferum*, *Anacardium occidentale*, *Magonia pubescens*, *Handroanthus ochraceus* and *Vatairea macrocarpa* were the species with best field establishment (see Table 4 and also Supplementary Material 1). The survival of woody individuals between the first and second year was in general similar to the one observed during the first year and relatively high for most species (Table 4).

After the first rainy season (6 months after sowing), tree seedling height was on average 7.2 ± 5.9 cm, and after the second rainy season (1.5 years after sowing) was 10.14 ± 8.2 cm. *Tachigali vulgaris*, *Buchenavia tomentosa*, *Solanum lycocarpum*, *Plathymenia reticulata*, *Eremanthus glomerulatus* and *Hymenaea stigonocarpa* were the fastest growing species (Table 4).

Among the grasses and shrub species evaluated by ground cover, *Andropogon fastigiatus*, *Aristida riparia*, *Schizachyrium sanguineum*, *Lepidaploa aurea*, *Stylosanthes* spp., *Achyrocline satureioides* and *Trachypogon spicatus* became best established in experimental areas, covering individually 2–30% of the soil. *A. fastigiatus* had the highest ground cover (30%) in the first year after seeding, whereas other species tended to increase their ground cover in the second year, especially *A. riparia*, *L. aurea* and *S. sanguineum* (Supplementary Material 1). Most grass and small shrub species maintained similar ground cover between the first and second year after sowing (Table 3).

Most of the species germinated successfully in the greenhouse (62 species, Table 1), but nine of those species did not produce seedlings under field conditions (e.g., *Byrsonima crassifolia*, *Cybistax antisiphilitica*, *A. crassiflora*). *Schefflera macrocarpa* had a mean of at least 20%

Table 4 Tree and shrub species for which seedlings were tagged and measured in four experimental direct seeding restoration sites in Central Brazil

Species	N	GHE%	Field emergence rainy season (%)	Survival first (%)	Survival first year (%)	Survival second year (%)	Height first year (cm)	Height second year (cm) ^b	Height third year (cm) ^b
Shrub species									
<i>Anacardium humile</i> ^a	2	63.0 ± 43.8	83.9 (67.8–100.0)	95.3 (91.1–99.4)	94.0 (91.5–92.3)	7.9 ± 6.9	7.9 ± 3.7	na	
<i>Bauhinia cf. dumosa</i>	1	5.0 ± 4.2	23.5	52.6	80.7 (76.9–83.3)	3.1 ± 2.5	6.2 ± 3.7	na	
<i>Jacaranda ulei</i>	2	8.0	0.0	na	na	na	na	na	
<i>Mimosa clausenii</i> ^a	2	22.6 ± 12.4	35.4 (0.3–70.6)	81.7 (68.3–95.1)	68.9 (21.4–100.0)	5.8 ± 15.4	4.2 ± 4.0	5.2 ± 9.2	
<i>Mimosa</i> sp.	1	0	12.2	69.2	na	2.2 ± 2.2	na	na	
<i>Parinari obtusifolia</i>	1	0	0.0	na	na	na	na	na	
<i>Senna alata</i>	2	13.0 ± 9.5	11.5 (3.7–19.2)	73.7 (67.6–79.7)	37.0 (15–56.3)	11.4 ± 10.6	10.0 ± 5.0	na	
<i>Zeyheria montana</i>	1	7.0	12.6	100.0	na	3.6 ± 1.5	na	na	
Tree species									
<i>Alibertia edulis</i>	1	1.0	2.5	66.7	na	4.3 ± 1.1	na	na	
<i>Amburana cearensis</i>	1	38.7 ± 26.0	6.9	33.3	na	10.6 ± 9.2	10.0	na	
<i>Anacardium occidentale</i> ^a	1	na	69.6	88.3	na	7.7 ± 7.3	8.11 ± 3.34	na	
<i>Anadenanthera colubrina</i>	4	73.0 ± 36.0	36.9 (6.7–71.1)	74.0 (50.0–100.0)	63.3 (25.0–100.0)	6.4 ± 4.7	9.0 ± 7.2	na	
<i>Annona crassiflora</i> ^c	3	26.0 ± 24.0	0.0	na	na	na	na	na	
<i>Aspidosperma macrocarpon</i> ^a	4	40.0 ± 32.9	34.5 (13.3–51.9)	89.6 (65.5–100.0)	80.0 (60.0–100.0)	9.0 ± 3.1	10.3 ± 4.4	na	
<i>Aspidosperma tomentosum</i>	2	46.0	10.0 (6.7–13.3)	100.0 (100.0–100.0)	80.0 (60.0–100.0)	7.8	7.4	na	
<i>Astronium fraxinifolium</i> ^a	2	79.3 ± 20.3	35.7 (0.0–71.4)	84.7	na	10.1 ± 5.8	na	na	
<i>Bowdichia virgilitoides</i>	2	na	12.1 (6.7–17.5)	68.8 (37.5–100.0)	55.0 (50.0–60.0)	3.6 ± 1.0	6.8 ± 2.1	na	
<i>Brosimum gaudichaudii</i> ^a	1	na	33.8	80.5	na	7.8 ± 2.1	8.29 ± 2.69	na	
<i>Buchenavia</i> sp.	2	0.0	7.2 (6.6–7.8)	61.4 (42.9–80.0)	55.0 (50.0–60.0)	5.3 ± 1.9	6.0 ± 3.0	na	
<i>Buchenavia tomentosa</i> ^a	1	30.0	27.8	96.8	86.11 (50.0–100.0)	14.5 ± 8.20	23.6 ± 12.8	25.4 ± 15.1	
<i>Byrsonima crassifolia</i> ^c	2	24.7 ± 14.4	0.0	na	na	na	na	na	
<i>Cecropia pachystachya</i>	1	0.02	0.0	na	na	na	na	na	
<i>Copaifera langsdorffii</i> ^a	5	44.6 ± 32.9	29.0 (17.4–50.3)	81.3 (34.8–100.0)	86.7 (60.0–100.0)	7.3 ± 4.1	7.1 ± 2.8	na	
<i>Cordia alliodora</i> ^a	1	27.0	31.7	83.5	na	9.7 ± 6.1	na	na	
<i>Cybistax antisyphilitica</i> ^c	2	49.0	0.0	na	na	na	na	na	
<i>Dalbergia miscolobium</i>	3	12.0	19.4 (2.8–49.3)	77.3 (57.3–100.0)	85.9 (64.7–100.0)	6.3 ± 2.7	9.3 ± 4.5	na	
<i>Devilla elliptica</i>	1	0.0	0.0	na	na	na	na	na	
<i>Dimorphandra mollis</i> ^a	2	6.0	30.8 (8.3–53.3)	80.0 (60.0–100.0)	90.5 (87.5–93.5)	5.4 ± 2.3	6.9 ± 2.8	na	
<i>Dipteryx alata</i> ^a	5	32.5 ± 44.5	36.5 (12.9–70.1)	93.5 (77.4–100.0)	89.1 (56.3–100.0)	9.3 ± 5.4	12.5 ± 6.2	12.8 ± 2.1	
<i>Enmotum nitens</i> ^c	1	na	0.8	50.0	na	4.0 ± 0.5	7.8 ± 3.9	na	
<i>Enterolobium contortisiliquum</i> ^a	3	3.7 ± 2.3	23.9 (5.7–39.2)	89.2 (71.9–100.0)	63.3 (25.0–100.0)	10.7 ± 6.3	13.6 ± 9.1	19.7 ± 3.5	
<i>Enterolobium gummiferum</i> ^a	1	na	79.6	91.6	63.3 (25.0–100.0)	17.5 ± 6.4	17.95 ± 5.93	na	
<i>Eremanthus glomerulatus</i>	1	32.0 ± 40.9	13.2	93.6	43.8 (0–70.0)	6.8 ± 6.5	14.4 ± 5.3	19.4 ± 17.4	

Table 4 continued

Species	N	GHE%	Field emergence (%) rainy season	Survival first year (%)	Survival second year (%)	Height first year (cm)	Height second year (cm) ^b	Height third year (cm) ^b
<i>Eriotheca pubescens</i> Endl.	3	33.5 ± 7.8	26.4 (15.0–45.9)	76.0 (55.6–100.0)	97.2 (91.7–100.0)	1.7 ± 1.0	4.5 ± 3.7	na
<i>Eugenia dzyentherica</i> ^a	4	8.0 ± 6.9	38.5 (3.5–69.3)	92.5 (70.0–100.0)	88.9 (66.7–100.0)	5.2 ± 3.6	7.0 ± 2.7	5.5 ± 5.4
<i>Guazuma ulmifolia</i>	2	12.0	0.0	na	na	na	na	na
<i>Hancornia speciosa</i>	1	63.0	15.8	36.8	na	6.9 ± 1.6	na	na
<i>Handroanthus ochraceus</i>	2	93.0	58.1 (17.3–98.9)	70.1 (40.2–100.0)	77.3 (60.0–90.0)	2.0 ± 1.7	3.1 ± 3.8	na
<i>Hymenaea stigonocarpa</i> ^a	5	47.5 ± 2.4	45.7 (5.8–83.3)	88.2 (73.3–100.0)	94.4 (83.3–100.0)	16.0 ± 8.2	21.2 ± 6.0	18.5 ± 13.2
<i>Jacaranda brasiliana</i>	4	35.3 ± 29.9	23.7 (8.5–37.8)	77.9 (57.1–94.8)	61.2 (0–100.0)	5.3 ± 6.9	9.4 ± 18.1	6.2 ± 4.2
<i>Kielmeyera coriacea</i>	3	28.0 ± 24.3	25.8 (5.5–48.1)	61.4 (30.6–83.9)	58.7 (47.4–71.4)	2.7 ± 1.9	3.6 ± 4.5	na
<i>Machaerium opacum</i>	3	3.6 ± 3.1	3.0 (0.6–7.2)	59.9 (20.0–80.0)	75.0 (50.0–100.0)	5.7 ± 2.2	10.2 ± 4.4	8.7 ± 13.4
<i>Magonia pubescens</i> ^a	6	62.0 ± 38.0	66.8 (34.2–100.0)	95.9 (91.7–100.0)	95.5 (87.5–100.0)	7.5 ± 5.0	9.9 ± 6.2	13.9 ± 4.6
<i>Myracrodruon urundeuva</i>	2	44.0 ± 49.4	62.6	76.6	67.2 (43.8–80.0)	3.7 ± 1.7	5.8 ± 2.5	na
<i>Plathymenia reticulata</i>	2	22.0	8.0 (7.0–8.9)	76.4 (73.7–79.2)	67.6 (42.8–100.0)	6.8 ± 3.4	14.6 ± 15.1	26.2 ± 15.7
<i>Qualea grandiflora</i>	1	na	50.7	71.9	na	8.5 ± 2.2	8.00 ± 3.04	na
<i>Schefflera macrocarpa</i>	2	20.0 ± 24.0	0.0	na	na	na	na	na
<i>Schinopsis brasiliensis</i>	1	4.5 ± 4.9	1.1	100.0	na	5.3 ± 4.6	7.3 ± 5.3	na
<i>Senegalia polyphylla</i>	1	55.7 ± 25.5	1.0	50.0	na	9.5	na	na
<i>Solanum lycocarpum</i>	5	23.0 ± 20.8	31.0 (1.3–63.7)	61.6 (20.0–88.0)	54.5 (30.6–69.1)	6.32 ± 9.3	15.1 ± 14.3	25.7 ± 13.3
<i>Stryphnodendron adstringens</i> ^a	3	11.3 ± 9.0	20.0 (4.2–39.0)	80.0 (40.0–100.0)	77.2 (50.0–100.0)	3.5 ± 1.9	4.9 ± 2.8	na
<i>Tabebuia aurea</i> S.Moore	1	na	63.7	74.0	na	2.4 ± 0.9	2.56 ± 1.13	na
<i>Tabebuia caraiba</i> ^a	1	39.0	34.2	88.2	na	6.0 ± 6.3	na	na
<i>Tachigali vulgaris</i>	2	44.5 ± 16.3	31.9 (31.3–32.5)	73.0 (58.0–88.0)	60.0 (32.3–83.3)	10.0 ± 6.0	36.4 ± 16.6	55.3 ± 25.5
<i>Terminalia argentea</i>	1	15.0	8.1	90.9	43.9 (20–86.7)	7.8 ± 4.7	5.5 ± 1.0	8.8 ± 1.8
<i>Terminalia fagifolia</i>	1	2.0	0.0	na	na	na	na	na
<i>Tibouchina candolleana</i>	2	31.7 ± 39.9	4.4 (0.0–8.9)	25.0	na	9.0	na	na
<i>Vatairea macrocarpa</i> ^a	1	13.0 ± 11.3	56.0	98.7	94.8 (88.9–100)	6.9 ± 2.4	7.4 ± 3.5	na

Number of experiments in which the species was planted (N); mean percentage seedling emergence in greenhouse (GHE) ± SD; mean field seedling emergence on the first rain season (0.5 year after sowing) (min – max); mean percentage of survival after first and second dry season (1 and 2 year after sowing) [mean (min – max)]; height one, two and third years after sowing na not available. Data on seedling height in second and third year are limited to seedling ages according to experiments. Some species were only sowed in the 2013 and 2014 experiments; therefore, data are not available for second/third year old growth

^a High emergence (>20%) and survival (>80%) species

^b Data on seedling height in 2nd and 3rd years are limited to seedling ages according to experiments. Some species were only sowed in the 2013 and 2014 experiments, therefore data is not available for second/third year old growth

^c 1.0–3.0% field emergence after first rainy season

seedling emergence in the greenhouse and no emergence in field conditions. On the other hand, some species failed to germinate in greenhouse conditions but successfully established seedlings in the field (e.g., *Mimosa* sp. and *Buchenavia* sp., Table 4). Emergence in both the field and in greenhouse was in general higher for tree species compared to shrubs and grasses (Table 2).

Discussion

Our results suggest that through direct seeding, it was possible to promote the establishment, at least for the first 2.5 years, of 62 trees, shrubs and grass species in relatively large areas of “Cerrado” previously dominated by invasive grasses. The planting cost per individual seed in direct seeding restoration programs is low, and low rates of both emergence and survival rates are considered normal (Palma and Laurance 2015). Some authors consider a 10% emergence rate an acceptable threshold (Engel and Parrotta 2001; Campos Filho et al. 2013), and this value is near the mean emergence rate (18%) obtained in most restoration projects around the world (Palma and Laurance 2015). We recorded 38 out of 58 woody species with at least a 10% emergence rate in the field; and identified 19 species with emergence rates above 20% associated with $\geq 80\%$ survival rate after the first year. These results indicate that these species can be successfully used in restoration practices through direct seeding. In addition, even species with low establishment rates can be useful to help compose the community, and increase diversity and richness. Some of them should be included in direct seeding restoration programs especially when seed collection and storage are not expensive.

Aside from these species, we can infer that other naturally abundant native species with high seed production might be good candidates for use in direct seeding restoration practice. Our data from greenhouse experiments indicate that there might be no direct relationship between seedling emergence in a greenhouse and seedling establishment in field conditions. This suggests that greenhouse experiments might not be worth performing in order to select species suitable to be planted in direct seeding restoration programs. Some studied species had good field establishment rates, but low emergence in the greenhouse. In contrast, other species had high emergence rates in greenhouse conditions, but low establishment rate in the field. In a greenhouse, seeds can be sowed in a precise depth, on a flat soil without lumps, protected from predation, and there is no water shortage. However, in a greenhouse, high humidity of air and soil may increase seed infection by pathogens, and environmental triggers for germination such as thermal and humidity variations are absent.

We found high values of seedling survival (80%) in the first 2.5 years, especially when compared to the 62% average survival of the seedling planting experiments for restoration identified in a recent review (Palma and Laurance 2015). Survival after the first dry season is a good parameter for long-term seedling establishment in savannas, where the length of the dry season can be a severe constraint to seedling survival due to water deficit in upper soil layers (Oliveira et al. 2005). Seedling survival between the first and second year was 92% on average for six “Cerrado” tree species in direct seeding experiments (Silva et al. 2015). For the 24 species for which we had survival data from the first to second year, survival rates varied from 54 to 97% (*Senna alata* and *Eriotheca pubescens*, respectively) with a mean of 75%. Seedlings’ tolerance to drought may also allow these plants to survive extreme climatic events that might occur due to climate change (Palma and Laurance 2015). Aside from water deficit during the dry season, the major causes of sapling death were probably dry spells during the rainy season (Assad et al. 1993), competition with invasive grasses, and ant herbivory.

The slow growth of “Cerrado” tree seedlings observed here (see also Silva et al. 2015) is partly due to high investment in below-ground tissues (De Castro and Kauffman 1998; Hoffmann and Franco 2003). Due to the slow aboveground growth of savanna tree species, tree seedlings will be affected by invasive grasses for years. Also, trees in savannas will not shade the ground enough to control invasive grasses. Thus, a key strategy for the success of restoration in non-forest ecosystems is the introduction of fast-growing herbaceous species, in high density, that can cover the soil and compete with invasive grasses (Filgueiras and Fagg 2008; Hulvey and Zavaleta 2012). Although herbaceous species, especially grasses, tend to have low seed germinability, they mostly have high seed production. Therefore, seed harvesting can represent a low-cost strategy in some sites/regions, allowing for high density of seeding. Our data show that species such as *L. aurea*, *A. riparia*, *A. fastigiatus*, *S. sanguineum*, *T. spicatus*, *Achyrocline satureoides* and *Stylosanthes* spp., grew fast and showed high proportion of ground cover, and some species even reproduced in the first rainy season after planting. These plants may help to structure the community, allowing other native species to establish and survive; they assume a similar role of fast-growing tree species commonly recommended for restoration and invasive grasses control in forest ecosystems (Rodrigues et al. 2009). Native shrub and herbs can readily cover the ground, which can help control invasive grasses by the temporal priority effect (Young et al. 2001) and can affect invasive grasses productivity (Corbin and D’Antonio 2004) and dominance.

This study presents information on a relatively large number of species, which represents a great increase in the otherwise scarce information on “Cerrado” species establishment in restoration areas, especially for herbaceous and shrub species. The information on fruiting period, fruit/seed processing method and field establishment in early years after sowing for these species can contribute to the research and practice on ecological restoration of “Cerrado” areas. These results inform restoration allowing for actions that include the use of different growth forms and species diversity, which might potentially create a complex native community.

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