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Re-vegetation with native species does not control the invasive *Ruellia simplex* in a floodplain forest in Florida, USA

Adrienne M. Smith, Carrie Reinhardt Adams, Christine Wiese & Sandra B. Wilson

Keywords
Floodplain forests; Invasive species; Mexican petunia; Re-vegetation; *Ruellia simplex*; Stormwater run-off

Nomenclature
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Smith, A.M. (corresponding author, amsmith@ufl.edu,)[1],
Reinhardt Adams, C. (rein0050@ufl.edu)[1],
Wiese, C. (hibiscus@ufl.edu)[1],
Wilson, S.B. (sbwilson@ufl.edu)[2]

[1]Department of Environmental Horticulture, University of Florida, P.O. Box 110675, Gainesville, FL 32611, USA;
[2]Department of Environmental Horticulture, University of Florida, P.O. Box 110670, Gainesville, FL 32611, USA

Abstract

Question: Planting or seeding native species after control of invasive species can limit re-invasion and hasten establishment of native species. *Ruellia simplex* (Mexican petunia) invades floodplain forests in Florida, and is controlled with glyphosate herbicide. Will herbicide application used to control this weed allow establishment of native vegetation and limit *R. simplex*?

Location: Floodplain forest altered by stormwater run-off, Lake Jesup Conservation Area, Sanford, FL, US.

Methods: We evaluated re-vegetation following herbicide application to control *R. simplex*. For re-vegetation, we planted or seeded native species (*Andropogon glomeratus, Juncus effusus, Panicum longifolium, Solidago fistulosa*) and measured stem density, percentage cover, above-ground biomass and species richness for 1 yr. We compared the results to those from control plots (i.e. no herbicide, no re-vegetation) and plots where *R. simplex* was sprayed with herbicide but not planted or seeded with native species.

Results: Unassisted re-colonization (i.e. plots where *R. simplex* was sprayed but not planted or seeded with native species) did not result in native plant restoration. Re-vegetation treatments (i.e. plots where *R. simplex* was sprayed and planted or seeded with native species) did not restore native vegetation; nor did re-vegetation treatments reduce *R. simplex* stem density, percentage cover or biomass compared to control plots. However, total species richness, including native and exotic species richness, increased in plots planted with a native plug mix compared to control plots (i.e. no herbicide, no re-vegetation). Native species failed to germinate in all seeding treatments. Plugs had adequate survival (2–57% depending on species) but did not prevent re-invasion of *R. simplex*. Re-invasion of *R. simplex* occurred in plots despite application of glyphosate herbicide and re-vegetation treatments.

Conclusions: Re-vegetation by seeding or planting did not establish native vegetation in the first year, instead, *R. simplex* reinvaded. Abiotic and biotic site conditions, e.g. invasive species propagule pressure and altered soil nutrients, may have limited seed germination and survival of planted seedlings. More research is necessary to determine if a reduction in invasive species propagules through repeated herbicide application coupled with planting native species results in native plant restoration in the longer term.

Introduction

Removal of the invasive species is the first step for restoration of invaded ecosystems. In some scenarios, native species subsequently establish from remnant individuals, disperse from other sites and/or emerge from the soil seed bank to effect restoration of a native plant community (Mitsch et al. 1998). Depending on unassisted re-colonization of native species after invasive removal is a succession-based approach to restoration practice that relies on

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these natural processes to return the system to its historical (pre-invasion) state (Suding et al. 2004). This approach is also referred to as passive ecological restoration, wherein recovery proceeds without active human intervention after weed removal (Zahawi et al. 2014).

Conversely, some invaded systems represent an alternative state, in which conversion to the original state is not achievable without considerable additional restoration efforts (Suding et al. 2004). For systems in this alternative state, return of the native plant community via passive restoration is limited by many factors, including soil degradation (Ren et al. 2008), limitation of native species propagules due to fragmented landscapes (Aronson & Galatowitsch 2008) and recruitment failure due to barriers associated with highly degraded soil conditions (Middleton 2003; Reinhardt Adams et al. 2015). Degraded soils can limit unassisted re-colonization by preventing native species germination, promoting the competitive ability of invasive species (Turner et al. 2011) and decreasing native species seedling establishment (Leishman et al. 2004). For many scenarios, unassisted re-colonization cannot be relied on as a restoration strategy.

Increasingly, restoration approaches for invaded lands follow invasive species control with active restoration of native species by seeding or planting (Holl & Aide 2011). Re-vegetation with vigorous native species may help mitigate the effect of degraded soils, and additionally may provide biotic resistance against invasive species (Bakker & Wilson 2004; Levine et al. 2004), including re-invasion, and thus achieve the ultimate goal of restoration of the native plant community. Despite the advantages of active restoration via re-vegetation, practical guidelines are lacking for many scenarios (Holzel et al. 2012). As is the case with many other restoration actions, research is needed to identify effective re-vegetation approaches that are economically feasible and practical for managers at all scales (Matzek et al. 2014).

Outcomes of re-vegetation efforts are affected by many choices, including planting densities, timing of planting and climatic conditions (Ruthrof et al. 2010; Woods et al. 2012). The decision to use direct seeding or to plant seedling plugs is also significant, because it influences restoration project cost (Palmerlee & Young 2010), likelihood and extent of establishment (Ruthrof et al. 2010) and genetic structure of the founding population (Breed et al. 2013). Experiments have optimized re-vegetation using either plugs (Quistberg & Stringham 2010; Ruthrof et al. 2013) or seeds (Vranjic et al. 2012; Ammondt et al. 2013; Enloe et al. 2013). Studies comparing plug and seed approaches with the same native species have, in some cases, found that planting plugs led to establishment of more individuals (Ruthrof et al. 2010) and resulted in higher native species diversity (Madruga-Andreu et al. 2011). Also, re-vegetation with higher species diversity can help to resist re-invasion (Peter & Burdick 2010), although some authors suggest that introducing exceptionally vigorous native species may be more effective against re-invasion (Johnson et al. 2010). Additional cost associated with any refinement of re-vegetation approaches (e.g. choosing plugs over seeds, planting more species) must be justified for any specific restoration scenario (Kettenring et al. 2014).

Research on restoration approaches for degraded systems that provide critical ecosystem services are urgent; logistically and economically feasible solutions are particularly elusive in this context. Approaches for restoration in riparian urban areas is especially critical, as these systems provide flood control (Sweeney et al. 2004; Felipe-Lucia et al. 2014), soil stability (Sweeney et al. 2004), habitat and removal of point and nonpoint source pollution (Felipe-Lucia et al. 2014); many of these services are linked to the presence of a stable native plant community. Native plant communities in these riparian wetlands are prone to external plant invasions as such systems often border urban development and experience high invasive species propagule pressure (Ramaswami & Sukumar 2014). Reduction in propagule pressure can limit invasions (Chadwell & Engelhardt 2008), but for invasive species in riparian wetlands for which stormwater is the primary dispersal pathway, this is particularly challenging because propagule sources are multiple and widespread.

We explored restoration approaches in floodplains invaded by *Ruellia simplex* (Mexican petunia) in Florida, which are typical of degraded floodplain forest habitats; they have elevated soil nutrients (Hupp 2007; Prince 2014), high invasive species propagule pressure and likely represent an alternative state that requires significant restoration intervention. Native to Mexico, *R. simplex* is a commonly planted herbaceous ornamental found throughout urban homeowner and commercial landscapes (http://florida.plantatlas.usf.edu, Accessed: Feb 2014). *Ruellia simplex* propagules have dispersed through stormwater run-off from urban areas to neighbouring floodplain forests, creating dense invasions (Langeland et al. 2008; Hupp et al. 2009). Propagule dispersal will likely continue due to use in homeowner landscapes and availability in the ornamental plant trade (Wirth et al. 2004). The state agency responsible for categorizing plant invasiveness in Florida recognizes *R. simplex* as a 'Category I invasive species' for displacing native plant communities (Smith et al. 2014); species that share this categorical classification include *Shinus terebinthifolius* (Brazilian peppertree), *Hydrilla verticillata* (hydrilla) and *Pueraria montana* var. *lobata* (kudzu). Recent research has found that herbicide application can reduce *R. simplex* populations (Reinhardt Adams et al. 2014), yet little native species re-colonization occurred (Reinhardt Adams et al. 2015). Low unassisted re-colonization may be related to continued invasive species propagule pressure. Therefore, *R. simplex*-invaded floodplains present a model system in which we can compare passive and active restoration by testing if re-vegetation following herbicide application promotes recovery from the degraded state.

In this study, we explored preliminary outcomes of four restoration approaches to determine which approach would most effectively suppress *R. simplex* and establish native species in a stormwater-influenced floodplain wetland. We tested the following hypotheses: (1) unassisted re-colonization is not sufficient to limit re-invasion and restore the native plant community; (2) seeding with a native species mix after herbicide application will limit *R. simplex* and restore the native plant community more effectively than seeding (after herbicide application) with two aggressive native species; and (3) planting plugs of native seedlings after herbicide application will limit *R. simplex* re-invasion and restore the native plant community more effectively than seeding treatments.

Methods

Study site

Our study was completed in a dense *R. simplex* invasion, with elevated soil nutrients and pH (Prince 2014), at the Lake Jesup Conservation Area (Sanford, Florida, USA). This site is typical of *R. simplex*-invaded Florida floodplains in soil nutrient composition, hydrology and geomorphic setting (Hupp 2007; Prince 2014). The Lake Jesup Conservation Area is comprised of 2.18 km^2 of land surrounding Lake Jesup, part of the Upper St. Johns watershed and listed as an impaired water body under section 303(d) of the Clean Water Act for exhibiting elevated ammonia, nitrogen and phosphorus levels, as well as low oxygen content (http://water.epa.gov/lawsregs/lawsguidance/cwa/tmdl/, Accessed: Dec 2014). Similar to many impaired waters in Florida (425 of the state's water bodies are nutrient-impaired; Badruzzaman et al. 2012), Lake Jesup receives stormwater run-off from Orlando, a major metropolitan city with a population of >2 000 000, and from four smaller cities with populations of >30 000 (http://www.sjrwmd.com/middlestjohnsriver/lakejesup.html, Accessed: Dec 2014; http://www.census.gov/en.html, Accessed: Dec 2013; Appendix S1). The conservation area is composed of many habitats, including hydric hammocks and floodplain wetlands. Hydric hammocks, dominated by *Juncus effusus* (common rush), *Quercus virginiana* (live oak), *Quercus laurifolia* (swamp laurel oak, and *Sabal palmetto* (cabbage palm) (FNAI 2010), form 'islands' throughout the conservation area, often along edges of floodplain forests. The re-vegetation experiment was conducted in a floodplain forest adjacent to a hydric hammock (28°45′33.174″ N, 81°12′42.446″ W). Dominant plant species found in the floodplain forest are the invasive *R. simplex* and native species including *Cyperus polystacyhyos* (many spike flat sedge), *Thalia geniculata* (alligator flag) and *Pontederia cordata* (pickerelweed). Soils are comprised of 100% felda and manatee mucky fine sands (http://websoilsurvey.sc.egov.usda.gov, Accessed: Dec 2013).

Data on natural site conditions (i.e. temperature, precipitation, light level, surface water depth, depth to groundwater) were collected to determine the possible natural abiotic influences on re-vegetation outcomes. Temperature was collected with a HOBO pendant temperature data logger (UA-001-64; Onset Computer Corp., Bourne, MA, US) from 1 Oct 2013 to 29 Oct 2014. Average maximum and minimum temperature ranged from warmest in Aug 2014 (36.7 and 24.3 °C, respectively) to coolest in Jan 2014 (20.7 and 8.2 °C, respectively; Fig. 1a). Precipitation was collected with a Data Logging Rain Gauge (RG3; Onset Computer Corp.) from 1 Oct 2013 to 29 Oct 2014, with average precipitation highest in Jul 2014 (366.5 mm) and lowest in Jan 2014 (0.6 mm; Fig. 1b). Light levels were collected using a fieldscout quantum foot–candle meter (Spectrum Technologies Inc., Planfield, IL, US) in the centre of each plot at 08:00 h monthly from 7 Aug 2013 to 3 Nov 2014, and ranged from highest in Aug 2013 (140 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and lowest in Nov 2013 (12 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Surface water depth was measured at three randomly selected areas in each plot monthly from 4 Oct 2013 to 3 Nov 2014, and ranged from 0 to 21 cm (Fig. 1c).

Depth to groundwater was measured using two PVC monitoring piezometers (Sprecher 2008), placed to capture the hydrological gradient, located both close to the hammock, in a drier area, and further from the hammock, in an area of shallow standing water. Depth to groundwater, measured as the distance from the soil surface to the water surface inside the piezometer, ranged from 0 cm (ground water at soil surface) to >22.5 cm (depth to ground water exceeded the depth of the well for several months).

Species studied

Using selection criteria based on information from the peer-reviewed literature and technical reports (Table 1), we chose native species that would likely establish under the site conditions. We used seeds and plug transplants from populations of *Andropogon glomeratus* (bushy bluestem grass), *Solidago fistulosa* (pine barren goldenrod), *Juncus effusus* and *Panicum longifolium* (redtop panic grass) growing in Florida. Native seeds were obtained from Ernst Conservation Seeds (Meadville, PA, US; *A. glomeratus*, *J. effusus*, *P. longifolium*) and The Natives, Inc. (Davenport, FL,

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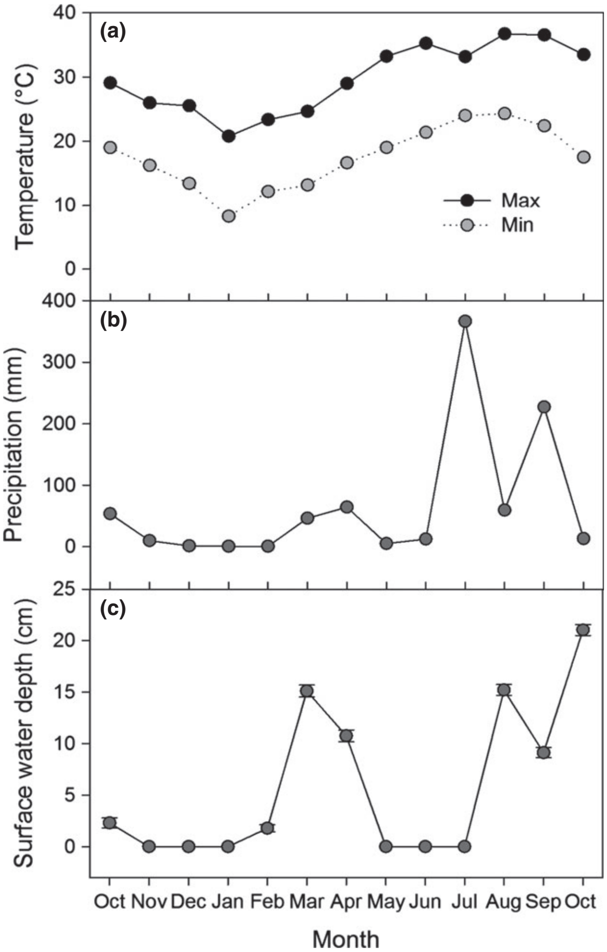

Fig. 1. Monthly mean (**a**) temperature, (**b**) precipitation and (**c**) surface water depth at the Lake Jesup Conservation Area (Sanford, FL, US) in a *R. simplex* invasion from Oct 2013 – Oct 2014.

US; *S. fistulosa*). Seed storage followed storage practices of the seed supplier: seeds were stored in a plastic bag in a refrigerator at 10 °C until use.

Experimental design

On 19 Sept 2012, plots were marked in each of four corners with 1.27-cm diameter rebar (steel reinforcing rod); to increase visibility, 1.5-m length PVC pipe was placed over each rebar. A total of 35 1.5 × 1.5 m plots, with 1-m buffers between plots, were installed. *Ruellia simplex* cover was dominant (90–100%) in all plots. A total of 35 plots allowed for seven replicates of each of the five treatments used: (1) no pretreatment herbicide and no re-vegetation (abbreviated as no PT–no reveg; control), (2) pretreatment herbicide and no re-vegetation (abbreviated as PT–no reveg; unassisted re-colonization), (3) pretreatment herbicide seeding with the two most vigorous native species (abbreviated as PT–TN seeds; containing *J. effusus* and *S. fisulosa*), (4) pretreatment herbicide and seeding with a native species mix (abbreviated as PT–NM seeds; containing *A. glomeratus*, *S. fistulosa*, *J. effusus* and *P. longifolium*), and (5) pretreatment herbicide and re-vegetation with plugs from a native species mix (abbreviated as PT–NM plugs; containing *A. glomeratus*, *S. fistulosa*, *J. effusus* and *P. longifolium*). Native species compositions were developed based upon results from a competition study between native species and *R. simplex* (Smith et al. 2015a).

The five treatments were randomly assigned to the 35 plots. On 7 Aug 2013, a 2% aquatic glyphosate solution (AquaPro; Dow Agrosciences LLC, Indianapolis, IN, US) at a rate of 222 ml per 11 L water, with 30 ml per 11 L water with surfactant (Induce; Helena Chemical Co., Collierville,

Table 1. Criteria for native species selection and justification for re-vegetation of formerly invaded *R. simplex* floodplains.

Criteria	Justification	Reference
Select species presence in local ecosystem	To ensure greatest chance of site-level adaptation	Garbisch (1986); Fischenich (2001)
Characteristic of vegetation present at the reference ecosystem	To ensure greatest chance of abiotic and biotic characteristics	White & Walker (1997)
Common, dominant or early successional	To ensure characteristic primary succession of site	Corr (2003); McClain et al. (2011)
Ability to withstand a wide range of water depths	To ensure survivability under seasonal flooding and drought conditions	Sheley et al. (2006)
Low maintenance species	To ensure minimal human intervention	Stark (1972)
High survival and growth rates in degraded systems	To ensure high survivability in disturbed areas	Goosem & Tucker (1995)
Species that are competitive under current site conditions	To ensure species competitiveness in current conditions	Fischenich (2001)
Species that are competitive during the seedling stage	To ensure establishment success of species despite the influence of abiotic factors	Oliveira et al. (2014)
Species that are competitive in disturbed environments	To ensure greatest chance of competiveness in altered habitats, including competition with invasive or exotic species	McClain et al. (2011)
Species that are readily available	To ensure practicality and availability for future use in restoration programmes	Kettenring et al. (2014)

TN, US) was applied with a backpack sprayer to all plots except the no PT–no reveg plots.

Using a replacement design (Hamilton 1994) to determine proportions of each native species to use in seed mixes, native seeds for seeding treatments were counted and weighed to give a rate of 600 pure live seed·m^{-2} (PLS·m^{-2}). Viability used to develop seeding rates was previously determined in Smith et al. (2015b). Practitioners typically seed wetlands at a rate of 300–600 PLS·m^{-2} (Mark Fiely, Ernst Conservation Seeds, pers. comm.); we chose to seed at 600 PLS·m^{-2} to provide abundant native propagules to the degraded floodplain, but still test a logistically and economically feasible seeding approach that practitioners could implement. Since burial may inhibit germination for these species (Wardrop & Brooks 1998; Mark Fiely, Ernst Conservation Seeds, pers. comm.), seeds were broadcast over the soil surface on 4 Nov 2013. This seeding practice mimicked seed rain events that occur during this time of year.

For the PT–NM plugs treatment, seeds from the same seed lot as seeding treatments were used to grow native species plugs. The plug production protocol is a typical method used for developing plugs for restoration plantings in the region. Seeds for each native species were broadcasted on the soil surface into half flats filled with Fafard germination mix (Sun Gro Horticulture, Agawam, MA, US) on 19 Mar 2013. On 9 Oct 2013, plugs were assembled by planting multiple individuals in a single plug with 52.7 × 26 cm plug trays with a single plug depth of 6 cm (Dillen product DPS72R propsht; Meyers Lawn & Garden, Middlefield, OH, US), using Atlas 7000 (Atlas Peat & Soil Inc., Boynton Beach, FL, US) as a filler. Plugs were top-dressed with 5 g Osmocote Plus Southern 15N–9P–12K (The Scotts Co., Marysville, OH, US) and watered for 30 s twice a day under a mist system in a greenhouse. Plugs were taken off the mist system 1 wk before planting to allow them to acclimatize to natural conditions. Plugs were then hand-watered once a day (ca. 2 s) until the soil was moist. On 4 Nov 2013, plug treatments (approximate heights: *A. glomeratus* = 20 cm, *J. effusus* = 50 cm, *P. longifolium* = 15 cm, *S. fistulosa* = 15 cm) were added to designated plots. Four plugs per species were placed in each plug treatment plot, randomized and installed in four rows, with each plant spaced 30 cm apart using a trowel, for a total of 16 plugs per plot (7 ind.·m^{-2}).

Data collection

To evaluate the effect of native species grown from seeds and plugs on suppression of *R. simplex*, *R. simplex* stem density was collected pre-treatment monthly from Aug 2013 to Nov 2013. After re-vegetation treatments were applied, stem density of all species (*A. glomeratus*, *J. effusus*, *P. longifolium*, *S. fistulosa*, *R. simplex*) was measured on a monthly basis, starting in Dec 2013 to Nov 2014. Stem density was collected by taking two subsamples in each plot, by randomly placing a 0.75 × 0.75 m PVC square, and averaging the subsamples. Percentage above-ground cover was collected every 3 mo in each plot for all species present in the plot, beginning 7 Aug 2013, using the following six visual cover classes from a modified Mueller-Dombois scale: 0 (0% cover), 1 (1–19%), 2 (20–39%), 3 (40–59%), 4 (60–79%), 5 (80–100%) (Mueller-Dombois & Ellenberg 1974). Using the percentage cover data, species richness of all native species (including the four planted native species), exotic species and total species were calculated.

At the conclusion of the study on 3 Nov 2014, above-ground biomass was collected from a single 15 × 15-cm subplot randomly located within each 1.5 × 1.5-m plot to allow for continued long-term monitoring. Biomass of *R. simplex*, *A. glomeratus*, *J. effusus*, *P. longifolium* and *S. fistulosa* was collected; in addition, biomass was collected for all other exotic species as a group and all other native species as a group. Samples were kept separate by plot and species/group classification. Samples were oven-dried in paper bags for 4 d at 70 °C and then weighed.

Statistical analyses

The experiment consisted of a randomized complete block design with five treatments. There were seven replicates of each treatment. Normality was checked by examining histograms and normality plots of the conditional residuals. Homogeneity of variance was examined by comparing boxplots. A one-way ANOVA was used to determine main effects of treatments on stem density, separately for each species at each month. Data were analysed in SAS (v 9.4; SAS Institute, Cary, NC, US) using the PROC MIXED command to estimate means. Additionally, the repeated measures was used to estimate main effects of treatments on stem density, percentage cover and species richness over time, separately for each species, using PROC MIXED and the repeated measures statement in SAS (v 9.4). Main effects of treatments on biomass were analysed with a one-way ANOVA, separately for each species, at the completion of the experiment. Data were analysed in SAS (v 9.4) using the PROC MIXED statement to estimate means. Tukey's HSD test was used to evaluate pair-wise comparisons with a significance level of $P = 0.05$.

Results

Herbicide application for all treatments (PT–no reveg, PT–TN seeds, PT–NM seeds, PT–NM plugs) produced the only significant treatment effect on *R. simplex* stem density (Fig. 2), percentage cover (Fig. 3a) and biomass (Fig. 3b);

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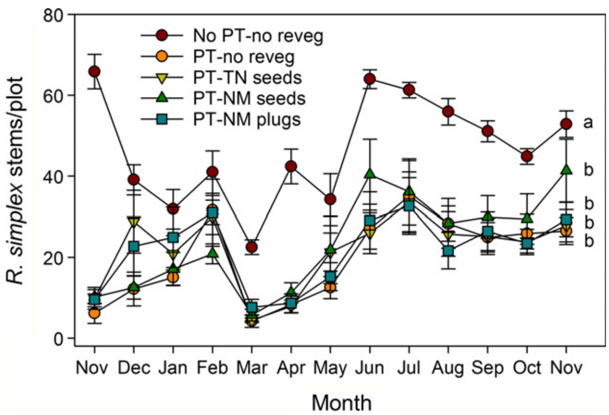

Fig. 2. Monthly means of *R. simplex* stems per plot (plot size = 0.56 m^2) over time from Nov 2013 – Nov 2014 at the Lake Jesup Conservation Area. Data represent means from two subsamples in each plot, and a total of seven replicates per treatment ± SE over time. Means with the same letter were not significantly different ($P < 0.05$). No PT–no reveg refers to no pretreatment herbicide and no re-vegetation (control). PT–no reveg refers to pretreatment herbicide and no re-vegetation (i.e. unassisted re-colonization). PT–TN seeds refers to pretreatment herbicide and seeding with two native species. PT–NM seeds refers to pretreatment herbicide and seeding with a native species mix. PT–NM plugs refers to pretreatment herbicide and re-vegetation with plugs from a native species mix.

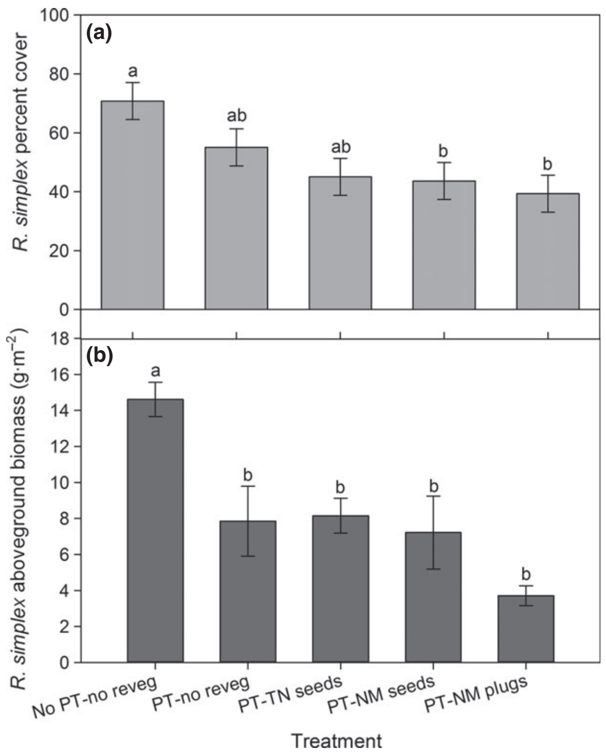

Fig. 3. Mean *R. simplex* (**a**) percentage cover from Nov 2013 – Nov 2014 and (**b**) above-ground biomass in Nov 2014 at the Lake Jesup Conservation Area. Percentage cover data were collected every 3 mo for 1 yr in each plot, and the subsamples collected at each data collection event were averaged over time. Above-ground biomass subsamples were collected on a 10% scale in each plot and averaged. Data represent means of seven replicates per treatment ± SE over time. Means with the same letter in the same graph were not significantly different ($P < 0.05$). No PT–no reveg refers to no pretreatment herbicide and no re-vegetation (control). PT–no reveg refers to pretreatment herbicide and no re-vegetation (i.e. unassisted re-colonization). PT–TN seeds refers to pretreatment herbicide and seeding with two native species. PT–NM seeds refers to pretreatment herbicide and seeding with a native species mix. PT–NM plugs refers to pretreatment herbicide and re-vegetation with plugs from a native species mix.

re-vegetation treatments (PT–TN seeds, PT–NM seeds, PT–NM plugs) did not affect *R. simplex* stem density, percentage cover and above-ground biomass. *Ruellia simplex* stem density was lower when sprayed with glyphosate compared to the control (Fig. 2), but there were no differences in stem density between re-vegetation treatments. Similarly, *R. simplex* percentage cover was reduced when plots were treated with glyphosate, but there were few differences in percentage cover between re-vegetation treatments (Fig. 3a). *Ruellia simplex* percentage cover in the PT–NM seeds and PT–NM plugs treatments was lower compared to the control, but was similar to the PT–no reveg and PT–TN seeds treatments. *Ruellia simplex* above-ground biomass was lower in plots treated with glyphosate than in the untreated control, but there were no differences in biomass between re-vegetation treatments (Fig. 3b).

Overall, native seeds did not germinate in seeding treatments (PT–TN seeds, PT–NM seeds). In the PT–NM plugs treatment, plug survival varied: *J. effusus* (46%), *P. longifolium* (57%), *S. fistulosa* (2%) and *A. glomeratus* (2%). Regardless of survival, plugs did not reduce *R. simplex* stem density, percentage cover or biomass. While re-vegetation approaches were not sufficient to suppress *R. simplex*, an increase in native, exotic and total species richness was noted in the plots with PT–NM plugs compared with the control plots (Fig. 4). Native (Fig. 4a) and total species (Fig. 4c) richness were highest in the PT–NM plugs treatment when compared to the No PT–no reveg and PT–TN seeds treatments. Native and total species richness were similar in both PT–no reveg and PT–NM seeds treatments, and in the No PT–no reveg and PT–TN seeds treatments. Exotic species richness (Fig. 4b) was higher in the PT–NM plugs treatment than the No PT–no reveg treatment, but was not different from PT–no reveg, PT–TN seeds and PT–NM seeds treatments. Although herbivory impact on plant establishment was not a focus of this study, observations indicated that herbivory from *Bos taurus* (cattle) affected all planted native species e.g. nibbled leaves or removal of entire plant; intense herbivory damage was prevalent on *S. fistulosa* and *A. glomeratus*, moderate on *J. effusus* and minimal on *P. longifolium*.

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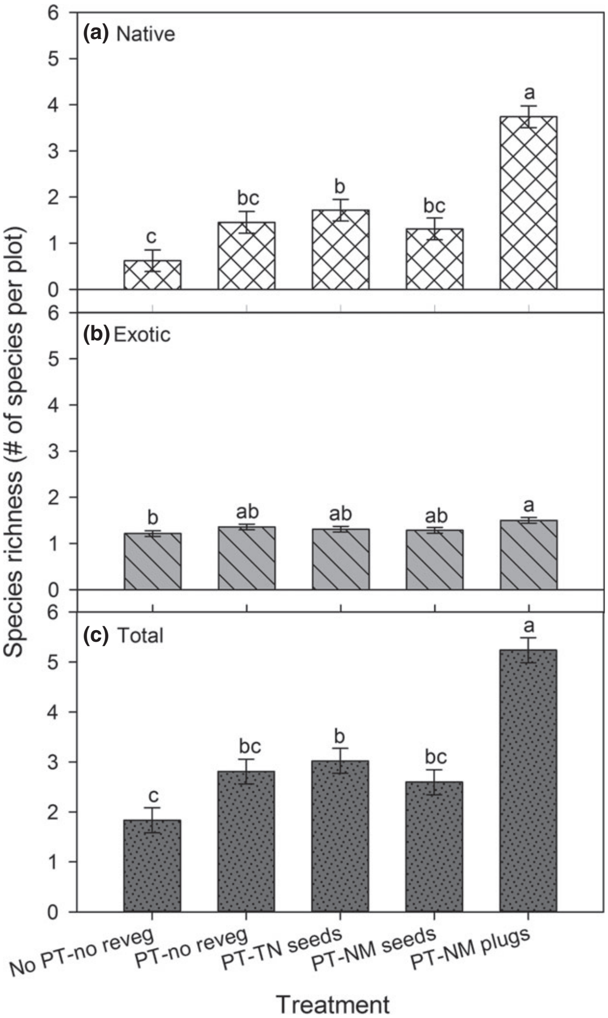

Fig. 4. Mean (**a**) native, (**b**) exotic and (**c**) total species richness (number species per plot) from Nov 2013 – Nov 2014 (plot size = 2.25 m^2) at the Lake Jesup Conservation Area. Data represent means of seven replicates per treatment ± SE over time. Means with the same letter in the same graph were not significantly different ($P < 0.05$). No PT–no reveg refers to no pretreatment herbicide and no re-vegetation (control). PT–no reveg refers to pretreatment herbicide and no re-vegetation (i.e. unassisted re-colonization). PT–TN seeds refers to pretreatment herbicide and seeding with two native species. PT–NM seeds refers to pretreatment herbicide and seeding with a native species mix. PT–NM plugs refers to pretreatment herbicide and rev-egetation with plugs from a native species mix.

Discussion

This study tested restoration approaches following herbicide application to control an invasive species, comparing passive restoration (unassisted re-colonization), to active restoration approaches (varying propagule type and species composition of seed mix). Our first assumption, that passive restoration via unassisted re-colonization was not sufficient to limit re-invasion and restore the native plant community, was correct; *R. simplex*, not native species, re-colonized 1 yr after control efforts. This preliminary finding supports our suggestion that the *R. simplex*-invaded floodplain forest is in an alternative state, where succession is not likely, thus active restoration via re-vegetation is required. Ultimately, after 1 yr, we did not observe restoration of the native plant community with any of our re-vegetation treatments. Species introduction and establishment, as studied here, has become a major issue in ecological restoration research (Holzel et al. 2012); when failure occurs, there is a unique opportunity to highlight factors that challenge re-vegetation in order to direct future approaches.

Despite seeding native species at the highest rate recommended by practitioners, we did not observe germination of any species sown in our field study; therefore, we could not test our second assumption that seeding a native species mix would limit *R. simplex* and restore the native plant community more effectively than seeding only two vigorous native species. This result was surprising, in that sowing seed (particularly with the species selected) is common in restoration practice, and is frequently relied upon for achieving re-vegetation goals. Sowing native species seed often results in establishment of the native plant community (Vranjic et al. 2012; Ammondt et al. 2013), yet in many scenarios seeding has also been unsuccessful (Ruwanza et al. 2013). Poor viability is sometimes blamed for a lack of seeding success (Farley et al. 2013; Le Stradic et al. 2014), however in this experiment seeding rates were adjusted to account for low viability in the seed lots (average germination determined in incubators ranged 6–24%; Smith et al. 2015b), so the lack of germination observed here should be attributed to factors other than low viability, possibly growing conditions at the site, competition from *R. simplex* or seed dormancy. Other authors note conditional dormancy in *Juncus* spp. and *Solidago* spp., but no dormancy in *Andropogon* spp. and *Panicum* spp. (Baskin & Baskin 1988).

The range of plug survival for native species in this study (2–57%) is reasonably typical of plugs planted for restoration: other reports of plug survival range from 20 to 90% (Quistberg & Stringham 2010; Ruthrof et al. 2013). Studies attribute low plug survival to factors including adverse growing conditions at the site (Le Stradic et al. 2014) and intense herbivory (Rodrigo et al. 2013). In this study, herbivory by *B. taurus* was an unanticipated constraint to plug establishment; *S. fistulosa* and *A. glomeratus* were heavily grazed and had the lowest plug survival, whereas *J. effusus* and *P. longifolium* were minimally grazed and had higher plug survival. Plug survival was high; because native species did not germinate in seeding treatments, we conclude that planting plugs would limit *R. simplex* and restore the

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native plant community more effectively than seeding treatments in a single year. Even when plugs established, there was no suppression of *R. simplex* within the 1-yr time frame of our experiment. When comparing native species establishment, planting plugs came closer to restoring the native plant community, but low establishment with both types of propagule suggests further intervention is necessary to improve native species establishment.

An interesting result in the PT–NM plugs treatment was an increase in exotic species richness, suggesting that a reduction in *R. simplex* facilitated novel exotic species colonization in the resultant bare soil. Suppression of the dominant invader may have facilitated these novel, or secondary, invasions (Flory & Bauer 2014): here, elevated soil nutrients and resultant bare ground, as well as a viable exotic species seed bank (Reinhardt Adams et al. 2015) and ideal germination conditions (Erfmeier et al. 2011), e.g. soil moisture from stagnant surface water, was sufficient for these secondary invasions to occur. Other studies that see a similar increase in secondary invasions suggest the need for effective control measures that not only limit the primary invasive species, but also potential secondary invasions that occur after removal of the initial invader (Ruwanza et al. 2013; Hudson et al. 2014).

Regardless of our treatments, *R. simplex* invasion remained a significant problem for restoration. Re-invasion occurred via germination from the seed bank, propagule (seed or rhizome fragments) arrival with stormwater or re-sprouting from rhizomes that remained viable even after herbicide application. While we did observe some post-planting germination of *R. simplex* from seeds, observations (7 mo after planting) determined that 97% of re-colonizing *R. simplex* originated from rhizome tips of plants that received the initial glyphosate application. Previous research noted that long-term chemical control is likely needed to control *R. simplex* (Reinhardt Adams et al. 2014). Further work to limit *R. simplex* re-colonization from rhizomes should evaluate growth regulator herbicides that target growing tips, as well as manual and mechanical removal of rhizomes (e.g. scraping).

We surmise that during this experiment, abiotic site conditions further compounded the lack of establishment of native plants and the subsequent persistence of the invasive *R. simplex*. Heavy rainfall resulted in high surface water in March 2014. Other authors note that heavy precipitation limits the effectiveness of direct seeding in two ways; first, seed may be lost from the site in high water conditions (Galatowitsch 2012), and second, flooding from rainfall may cause anaerobic stress and inhibit germination (Smith et al. 2002; Kolb & Joly 2010). Because our species are adapted to establishment in wet conditions (classified as obligate: *J. effusus, P. longifolium*; or facultative wetland species: *A. glomeratus, S. fistulosa*), we expected germination; however, this prolonged high water event likely created saturated soil conditions that inhibit germination of even obligate and facultative wetland species (Smith et al. 2002).

In addition to soil hydrology, soil degradation, particularly elevated nutrients from anthropogenic sources, is another factor that may have limited germination in this study. McCormick & Gibble (2014) suggested that nutrient-enriched soils may have inhibited germination of native species from the seed bank in wetlands of the Florida Everglades. Nutrient enrichment could create growing conditions that confer a competitive advantage to *R. simplex* dominance over native species. In fact, elevated nutrients associated with urban development in the associated watershed have been linked to patterns of dominance for other problematic invasive species, including *Phragmites australis* (common reed; McCormick et al. 2010) and *Phalaris arundinacea* (reed canary grass; Kercher & Zedler 2004). Similarly, *R. simplex* invasions exist primarily in floodplain forests that receive stormwater run-off (Hupp 2007), a consequence of which can be elevated soil nutrients (Leishman et al. 2004). Observational studies further link *R. simplex* dominance and elevated soil nutrient levels (Prince 2014). However, these studies do not conclude whether *R. simplex* dominance is due to a lack of native species germination or elevated soil nutrients that allow *R. simplex* to establish and out-compete native species.

Our efforts to re-vegetate native species following initial control were ineffective, and no treatment provided enhanced biotic resistance to prevent re-invasion. Accounts of rapid restoration of the native plant community are rare (but see Ammondt et al. 2013). It could be argued that expectation of re-vegetation success within 1 yr is unrealistic, and even 2–3 yr is unlikely (Martin & Wilsey 2014). Re-vegetation efforts for *R. simplex*-invaded floodplains may be more successful over a longer time frame and with (1) multiple introductions of native species propagules over several years (Woods et al. 2012) and (2) follow up selective control of the invasive species during initial stages of native species germination and establishment (Bohnen & Galatowitsch 2005; Enloe et al. 2013). Further, we recommend experiments at multiple sites and empirical tests at the landscape level to assess feasibility and success of these approaches (Ogden & Rejmanek 2005). Walker et al. (2014) points to consideration of the severity of disturbance as critical for design of optimal restoration activities; active restoration with a more intense level of intervention than tested here may be required for restoration of the native plant community in this highly disturbed setting.

Guided by requests for research on cost-effective and feasible management strategies (Matzek et al. 2014), this work tested the most straightforward approach for restoration of a native plant community. It is our responsibility as researchers to learn from these failures (D'Antonio & Meyerson 2002); ultimately, development of effective re-vegetation methods will proceed more rapidly by building on our results.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. The study site in a floodplain forest at the Lake Jesup Conservation Area.

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