SHST
Horticulture and Forestry Society of Transylvania

Bulu YI *et al.* (2023)
Notulae Scientia Biologicae
Volume 15, Issue 1, Article number 11380
DOI:10.15835/nsb15111380
Research Article

NSB
Notulae Scientia Biologicae

Soil seed bank studies of *Tithonia rotundifolia* invaded fallow land and competitive association with *Chromolaena odorata*

Yetunde I. BULU*, Rilwan O. AHMED, Opefoluwa D. FADAYOMI, Otitoloju KEKERE

Adekunle Ajasin University, Department of Plant Science and Biotechnology, Akungba-Akoko, Nigeria; yetunde.bulu@aaua.edu.ng (corresponding author); optimalrilwan@gmail.com; opeoluwafadayomi@yahoo.com; otito.kekere@aaua.edu.ng

Abstract

In Nigeria, *Chromolaena odorata* (L.) R. M. King and H. Rob and *Tithonia rotundifolia* (Mill.) S. F. Blake, are exotic invasive weeds, but a gradual decrease in the population of *C. odorata* with the rapid invasion of *T. rotundifolia* is now observed. Therefore, this study investigated the adaptive features of each weed in competition, with a further determination of seedling recruitment from the soil seed bank of plots invaded by *T. rotundifolia*. Field sampling was carried out in 10 plots: *T. rotundifolia* invaded plots and low or uninvaded plots in co-existing with other plants using 10 m x 10 m quadrats. The readily germinable seed species composition and the Sorensen index of similarity between the seed bank and their above ground vegetation were determined. Competition Series Experiment was also conducted for the two plants. *Mariscus alternifolius* (227) and *Oldenlandia corymbosa* (358) were the most abundant species in the seed bank while *T. rotundifolia* recruited 25 individuals. Low similarity index existed between the seed bank and the standing vegetation of the invaded and uninvaded plots. *T. rotundifolia* had improved growth in heteroculture with *C. odorata* over when in monoculture. However, a reduction in growth of *C. odorata* occurred when in competitive association with *T. rotundifolia* compared to when in monoculture. *T. rotundifolia* had competitive advantage over *C. odorata.*

Keywords: invasive plant species; seedling recruitment; soil seed bank

Introduction

In recent times, a lot of attention has been given to the harmful effect of invasive alien plant species on the functioning of ecosystems (Zhang *et al.*, 2019). Among the mechanisms enhancing successful naturalization and invasion of a new environment by alien plant species, escape from their natural enemies (competitors, herbivores and pathogens) and ability to allocate resources to traits that promote greater competitive advantage, such as size and fecundity, are viewed as characters conveying advantage on them (Joshi and Vrieling, 2005).

Aside the formation of a mono-specific stand, the ability to establish a reserve of seeds in the soil seed bank in their new environment can contribute significantly to their successful naturalization and invasion potential (Gioria *et al.*, 2021). Giving the function of the soil seed bank as source of propagules, genetic diversity

Received: 15 Nov 2022. Received in revised form: 01 Jan 2023. Accepted: 01 Mar 2023. Published online: 16 MAr 2023.
From Volume 13, Issue 1, 2021, Notulae Scientia Biologicae journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers.

and a mechanism of safeguarding against reproductive failure and unfavorable environmental conditions (Larson and Funk, 2016; Gioria *et al.*, 2021), early seed sets and their storage in the seed bank may give an alien invasive plant a hedge over the native plants.

In response to invasion from an alien species, the seed bank may likewise serve a protective role to the native plants by preventing their extinction by functioning as source of seed storage and recruitments for species absent from the aboveground vegetation during the process of revegetation of the invaded community. So far, the effect of invasive plant species on plant communities and biodiversity has only been viewed by investigating changes in the above ground species richness with little information on the impact or significance of the seed bank. Therefore, investigating the changes occurring in the seed bank of exotic invasive species and native species in invaded communities is essential to predict the recruitment potential of these species from the seed bank and in understanding the roles of the seed bank in invasion success.

Chromolaena odorata (L.) R. M. King and H. Rob. and *Tithonia rotundifolia* (Mill.) S. F. Blake are invasive alien weeds from Mexico that are widely distributed in the south-western part of Nigeria. *C. odorata* is a perennial herb that grows up to 2.5 m tall in open areas. It is hairy and glandular with leaves that are opposite, triangular to elliptical with serrated edges. The white to pale pink tubular flowers are in panicles of 10 to 35 flowers that form at the ends of branches. *T. rotundifolia* on the other hand is an erect annual herb with yellow or orange red blooms that contains between 8 and l0 ray florets and between 65 and 90 disk florets in its capitulum (Adebowale and Olorode, 2005; Olorode *et al*., 2011). *C. odorata* was reportedly introduced into the country from Sri Lanka in 1937 and has currently reached an alarming population (Uyi et al., 2013; Uyi and Igbinosa, 2013). On the other hand, *T. rotundifolia* is gaining increasing attention because of the formation of dense mono-specific stand and an ability to outcompete native vegetation (Adebowale and Olorode, 2005).

The successful establishment and invasion of *T. rotundifolia* and *C. odorata* in new environment have been attributed to their fast growth rates, early maturity and large seed sets relative to native plant species. Currently, *T. rotundifolia* is prominently observed in the country with a consequent gradual decrease in the population of *C. odorata* especially in the south western part of the country where it once dominated (Adebowale and Olorode, 2005). In this study, we hypothesized that *T. rotundifolia* outcompete *C. odorata* and form a large and persistent seed bank which will enhance its establishment and invasiveness in any new environment. This study therefore investigated the relative reciprocal performance of the two invasive species viz *T. rotundifolia* and *C. odorata* on each other. The study also examined the characteristics of the seed bank of *T. rotundifolia* invaded and uninvaded plots.

Materials and Methods

Vegetation analysis and soil seed bank determination

Soil seed bank studies were carried out at the screenhouse of the Department of Plant Science and Biotechnology (PSB), Adekunle Ajasin University (AAUA), Nigeria. A recognisance study was first embarked upon in the Northern part of Ondo State, South Western Nigeria, to identify areas of vegetation cover with high population of *T. rotundifolia* in co-existence with *C. odorata* and other plant species. Consequently, a field survey was embarked upon in fallow land vegetation along Akure-Akungba expressway in Ondo State, Nigeria (07°16'34.0'N; 005°17'48.9E to 07°27'11.6'N; 005°43'47.0E). Sampling points were systematically placed at every 5 km distance along the expressway from Akungba-Akoko (07°16'34.0'N; 005°17'48.9E) to Akure (07°27'11.6'N; 005°43'47.0E) between July and December, 2020. At each point, two sampling plots were selected in fallow land vegetation in the area; one dominated by *T. rotundifolia* (invaded plot) and another with low population of *T. rotundifolia* in co-existence with *C. odorata* and other plant species (uninvaded plot). A total of ten plots were identified with six designated as invaded plots (plots 1, 2, 3 4, 5 and 10) and four uninvaded plots (plots 6, 7, 8 and 9). In each sampling plot, a three 10 m x 10 m quadrat was laid out randomly for determination of floristic composition with identification of plants to species level. Species whose identities were in doubt were collected and taken to the Department of PSB Herbarium for proper identification. Three replicate soil samples were also collected each at depths of 0-15 cm and 15-30 cm, taken to the Laboratory of the Department of PSB and air-dried. The soils were filled into perforated plastic pots and the direct germination method of Thompson and Grime (1979) was used to assess the readily germinable seed species composition. The relative abundance of plant species or families on the standing vegetation and seed bank was estimated as the percentage each species or families contributed to the total number of individuals present. The Sorensen Index of Similarity between the above ground vegetation and their seed bank was estimated according to Chao *et al*. (2005).

Plant competition experiment

Uniform seedlings (relatively equal size) of *C. odorata* and *T. rotundifolia* were collected from an open field around the sampling area with known history of clearing four weeks prior to the commencement of the experiment. The seedlings were transplanted into perforated polythene pots (30 cm by 25 cm) filled with top soil collected from the experimental field of the Department of PSB which was a nutrient-rich sandy-loam soil according to Kekere *et al*. (2020). Each pot replicated five times, contained a total of 6 seedlings in monoculture or heteroculture in a competition series experiment viz: T1 = 6 *C. odorata*: 0 *T. rotundifolia*; T2 = 5 *C. odorata*: 1 *T. rotundifolia*; T3 = 4 *C. odorata*: 2 *T. rotundifolia*; T4 = 3 *C. odorata*: 3 *T. rotundifolia*; T5 = 2 *C. odorata*: 4 *T. rotundifolia*; T6 = 1 *C. odorata*: 5 *T. rotundifolia*; and T7 = 0 *C. odorata: 6 T. rotundifolia.* The pots were arranged in a completely randomized experimental design in the screen house of the Department of PSB.

The experiment lasted for 12 weeks. Plant stem girth was measured with vernier calliper at the 2 cm point from the base of the stem while a meter rule was used to measure the height from the soil surface to the apical bud. Plant leaves were counted and the leaf area determined with the Leaf Area Meter (LI-COR 300 model). At 12 weeks after planting, the plants were carefully uprooted and the primary roots counted with their lengths measured. The shoot lateral branches were also counted. Fresh and dry mass of plant parts were measured and the moisture content calculated as $\frac{fresh\ weight - dry\ weight}{fresh\ weight} x100$ while the relative growth rate was accounted for according to Hoffmann and Poorter (2002) with the formula: $\frac{\ln w2 - \ln w1}{t2 - t1}$ where w1 and w2 are the means of the natural logarithm of transformed plant weight.

All data obtained were subjected to one-way ANOVA. Statistical means were separated with New Duncan Multiple Range test at 95% level of significance using the Statistical Package for Social Sciences (SPSS software, version 24.0).

Results

Species composition of the standing vegetation

Forty-four plant species belonging to 15 families were identified in the ten plots of the standing vegetation. The plant habits as shown in Table 1, comprised 26 herbs (59.10%), 10 shrubs (22.70%), 7 grasses (15.90%) and 1 climber (2.30%). On the invaded plots, plants belonged to six families (Figure 1) contributed plant species to the above ground vegetation with the Poaceae having the highest number of individuals (33.33%). Each of the Fabaceae, Amaranthaceae and Euphorbiaceae families had a relative abundance (RA) of 16.67%. Other families had a RA of 8.33% and below. Similarly, fourteen families were enumerated on the uninvaded plots. However, the Fabaceae family had the highest RA (21.86%) followed by the Poaceae and Asteraceae with 12.50% each. Meanwhile, the relative abundance of the Cucurbitaceae, Portulacaceae, Euphorbiaceae and others ranged between 3.13% and 9.38%.

Table 1. Plant species composition on the standing vegetation of the study plots

S/N	Species	Family	Habit	1	2	3	4	5	6	7	8	9	10
1	*Aeschynomene indica*	Fabaceae	Shrub	-	-	-	-	+	+	-	-	-	-
2	*Amaranthus viridis*	Amaranthaceae	Herb	-	-	-	+	-	-	-	-	-	-
3	*Andropogon tectorum*	Poaceae	Grass	-	+	-	-	-	+	-	-	-	-
4	*Argeratum conyzoides*	Asteraceae	Herb	-	-	-	-	-	-	+	-	-	-
5	*Blumea aurita*	Asteraceae	Herb	-	-	-	+	-	-	+	-	-	-
6	*Brachiaria jubata*	Poaceae	Grass	-	+	-	-	-	-	-	-	-	-
7	*Calopogonium spp*	Fabaceae	Herb	+	+	-	-	+	+	-	-	-	+
8	*Celosia argentea*	Amaranthaceae	Herb	-	-	-	+	-	-	-	-	-	-
9	*Centrosema pubescens*	Fabaceae	Herb	-	-	+	-	-	+	-	+	-	-
10	*Chamaecrista rotundifolia*	Fabaceae	Shrub	-	-	-	-	-	-	+	-	-	-
11	*Chromolaena odorata*	Asteraceae	Shrub	-	-	-	-	-	-	-	+	-	-
12	*Digitaria gayana*	Poaceae	Grass	-	-	-	-	-	+	-	-	-	-
13	*Cissus quadragullaris*	Vitaceae	Climber	-	-	-	-	-	-	-	+	-	+
14	*Corchorus spp*	Malvaceae	Herb	+	-	-	-	-	-	-	-	-	-
15	*Desimodium spp*	Fabaceae	Shrub	-	-	-	-	-	+	-	-	-	-
16	*Eleutheranthera ruderalis*	Asteraceae	Herb	-	-	+	-	-	-	-	-	-	-
17	*Euphorbia alta*	Euphorbiaceae	Herb	-	-	-	-	-	-	-	-	+	-
18	*Euphorbia heterophylla*	Euphorbiaceae	Herb	-	-	+	-	+	-	-	-	-	-
19	*Euphorbia hirta*	Euphorbiaceae	Herb	-	-	-	+	-	-	-	-	-	-
20	*Fleurya aestuans*	Urticaceae	Herb	-	-	+	-	-	-	-	-	-	-
21	*Gomphrena celosioides*	Amaranthaceae	Herb	-	-	-	-	-	-	+	-	+	-
22	*Indigofera indica*	Fabaceae	Shrub	-	-	-	-	-	-	-	+	-	-
23	*Luffa cylindrical*	Cucurbitaceae	Herb	-	-	-	-	-	-	-	-	+	-
24	*Mariscus alterniphorus*	Cyperaceae	Herb	-	-	+	-	-	-	-	-	-	+
25	*Melanthera scanden*	Asteraceae	Herb	-	-	+	-	-	-	-	-	-	-
26	*Mimosa invisa*	Fabaceae	Shrub	-	-	-	-	+	-	-	+	+	-
27	*Mitracapous villosus*	Rubiaceaea	Herb	-	-	-	-	-	-	-	-	-	+
28	*Oldenlandia corymbosa*	Rubiaceae	Herb	-	-	-	-	-	-	+	-	-	+
29	*Panicum maximum*	Poaceae	Grass	+	+	-	-	+	-	-	+	-	+
30	*Paspalum scrobiculatum*	Poaceae	Grass	-	-	-	-	-	-	-	-	-	+
31	*Peperomia pellucida*	Piperaceae	Herb	-	-	+	+	-	-	-	-	-	-
32	*Phyallathus amarus*	Euphorbiaceae	Herb	+	+	-	-	-	-	-	-	-	-
33	*Physalis angulata*	Solanaceae	Herb	+	-	-	-	-	-	-	-	-	-
34	*Physalis micrantha*	Solanaceae	Herb	-	-	-	-	-	-	-	-	+	-
35	*Pupalia lappacea*	Amaranthaceae	Herb	-	-	-	-	-	-	-	-	+	-
36	*Rhynchelytrum repens*	Poaceae	Grass	+	-	-	-	-	-	-	-	-	-
37	*Richadia brasilensis*	Rubiaceae	Herb	+	-	-	-	-	-	-	-	-	-
38	*Senna hirsute*	Fabaceae	Shrub	-	-	-	-	-	-	-	-	+	-
39	*Sida acuta*	Malvaceae	Shrub	+	-	-	-	-	-	+	-	-	-
40	*Spermacoce latifolia*	Rubiaceae	Herb	-	-	-	-	-	-	+	-	-	+
41	*Sporobolus pyramidalis*	Poaceae	Grass	-	-	-	-	-	+	-	-	-	-
42	*Talinum trangularae*	Portulacaceae	Herb	-	-	-	+	-	-	-	-	-	-
43	*Tithonia rotundifolia*	Asteraceae	Shrub	+	+	+	+	+	-	-	-	-	+
44	*Urena lobata*	Malvaceae	Shrub	-	-	-	-	-	-	-	-	+	+

Key + = Present; - = Absent

Plant species composition of soil seed bank

Seedling emergence from the soil seed bank at 0 - 15 cm and 15 – 30 cm depths are shown in Figures 2 and 4. At 0-15 cm depth, there were 20 herbs, 10 grasses and 4 shrubs constituting 58.4% herbs, 29.4% grasses and 11.8% shrubs respectively. The plants belonged to 14 families each on invaded and uninvaded plots with Poaceae having the highest RA of 15% and 30% on invaded and uninvaded plots respectively.

Other families ranged between 10% and 5% for invaded plots, and 10% and 3.33 for uninvaded plots. The plant species composition from the soil seed bank at 15-30 cm depth is shown in Figure 3.

A total of 29 species composing of 18 herbs, 8 grasses and 3 shrubs were found, constituting 62.07%, 27.59% and 10.54% respectively. Each of the invaded and uninvaded plots had plant species found in 13 families. Poaceae had the highest RA of 28% on uninvaded plots and 35% on invaded plots. On the uninvaded plots, other families had 4-12% RA while 4-10% was recorded on the invaded plots.

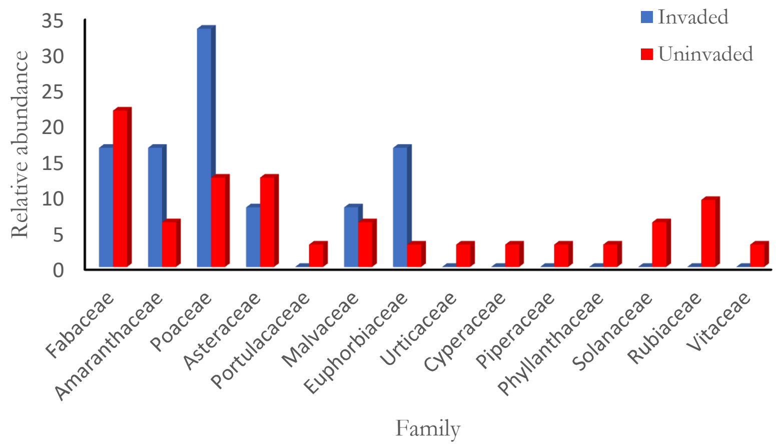

Figure 1. Families of plant species in the standing vegetation of the studied plots

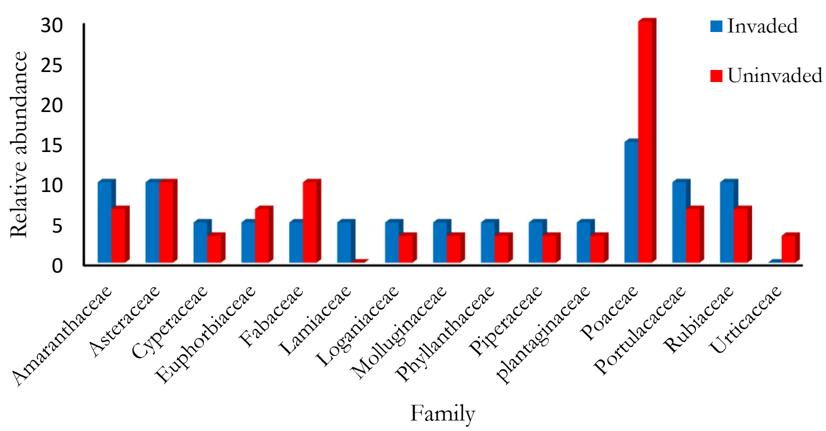

Figure 2. Families of plant species recruited from the seed bank at 0-15 cm depth

Seedling recruitment from the soil seed bank

Figure 4 shows the relative abundance of seedling recruited from the soil seed bank from the invaded and uninvaded plots at 0-15 cm and 15-30 cm depths. On the uninvaded plots, soils collected at 0-15 cm and 15-30 cm depths had the highest number of seedling recruits from seed bank at plot 7 (43.63 and 34.12 respectively) and lowest at plot 8 (3.73 and 2.56 respectively). On the invaded plots, seedling recruitment from the seed bank peaked at plot 3 (10.58 and 16. 97) and plot 5 (8.29 and 16.97) for soils collected at 0-15 and 15-30 cm depths respectively.

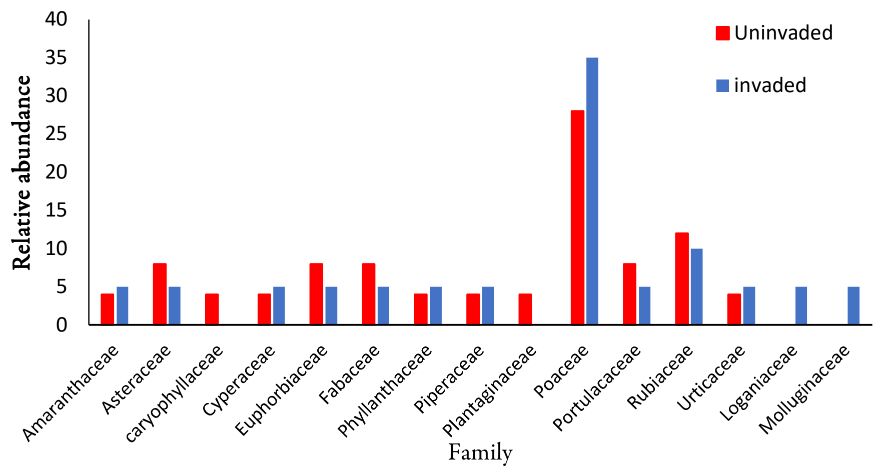

Figure 3. Families of plant species recruited from the seed bank at 15-30 cm depth

At both the invaded and uninvaded plots, *Mariscus alternifolius* and *Oldenlandia corymbosa* were the most abundant species in the seed bank. The number of seedlings recruited from the soil seed bank from the invaded and uninvaded plots include *O. corymbosa* (73 and 513 seedlings), *M. alternifolius* (128 and 82), *Eleusine indica* (24 and 11), *Panicum maximum* (38 and 2), *Mitracarpus villosus* (33 and 31), *Celosia leptostachya* (80 and 3), and *T. rotundifolia* (13 and 12) respectively.

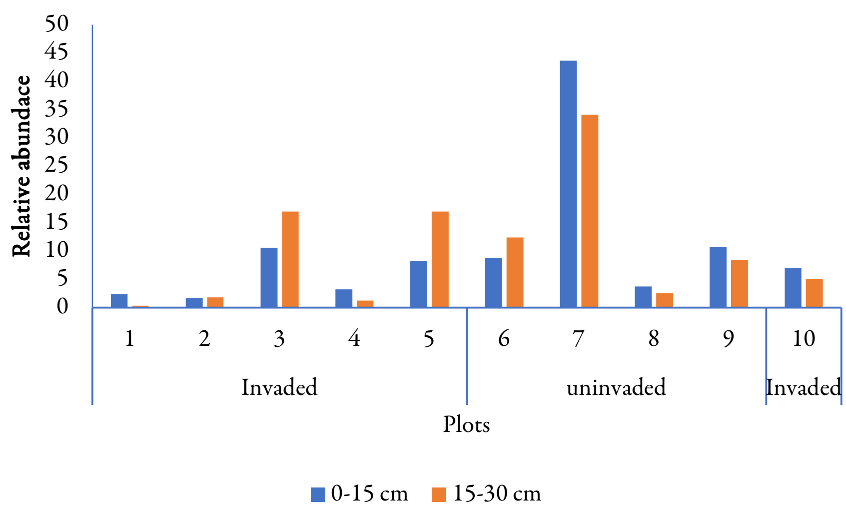

Figure 4. Relative abundance of species recruited from the soil seed bank

Similarity in species composition (standing vegetation and seed banks)

Table 2 shows the Sorensen Similarity Index between the soil seed bank at different depths (0-15 cm and 15-30 cm) on the invaded and uninvaded plots. High similarity index was recorded between 0-15 cm and 15-30 cm depths on the invaded plots at plot three (0.78), five (0.63) and ten (0.57) but there was no similarity in plot 1 as similarity index was 0.00. In addition, high similarity index ranging from 0.46 to 0.61 was recorded between 0-15 cm and 15-30 cm depths for plant species composition on the uninvaded plots. The similarity index in species composition between soil seed bank at both depths and the standing vegetation gave low values for both invaded and uninvaded plots.

Table 2. Similarity index in species composition at different soil depths and between standing vegetation

Plot No	Plot type	Similarity index		
		0-15 cm and 15-30 cm soil depth	Standing vegetation and 0-15 cm soil depth	Standing vegetation and 15-30 cm soil depth
1	Invaded	0.00	0.29	0.00
2	Invaded	0.22	0.20	0.44
3	Invaded	0.78	0.17	0.00
4	Invaded	0.36	0.40	0.22
5	Invaded	0.63	0.00	0.00
6	Uninvaded	0.61	0.20	0.07
7	Uninvaded	0.54	0.37	0.37
8	Uninvaded	0.57	0.40	0.31
9	Uninvaded	0.46	0.14	0.00
10	Invaded	0.57	0.14	0.00

Growth parameters of C. odorata and T. rotundifolia under different levels of interspecific competition

The height of *C. odorata* was significantly reduced by higher density of *T. rotundifolia* (Table 3). For example, the lowest value of 33.00 cm and 33.25 cm were recorded at ratios 1:5 and 2:4 *C. odorata* and *T. rotundifolia* respectively. *C. odorata* however had the highest height (40.08cm) when the mixture of the two plants was of equal number. Other growth parameters including stem girth (1.80 cm), number of leaves (16.58) and leaf area (33.04 cm) of *C. odorata* were highest when grown alone in pots than in competition with *T. rotundifolia*.

The height of *T. rotundifolia* increased with increase ratio of *C. odorata* such that the highest height of 106.75 cm was recorded at *T. rotundifolia* and *C. odorata* density of ratio 1:5. Except for the number of leaves where the highest value of 26.42 was recorded at *T. rotundifolia* and *C. odorata* 3:3 ratio, all other parameters including the stem girth (3.80 cm) and the leaf area (220.28 cm^2) were highest at 1:5 ratio.

In the absence of *T. rotundifolia*, *C. odorata* had significantly higher number of roots than when *T. rotundifolia* was present (Table 4). A significant reduction in the number of roots was recorded in *C. odorata* with increased density of *T. rotundifolia* in the pots. A similar trend was recorded in the length of the roots of *C. odorata* where a significant high value of 15. 08 cm was obtained in the absence of *T. rotundifolia.* Significantly higher value of 14.75 was recorded for the number of roots of *T. rotundifolia* when it occurred in equal density with *C. odorata* than when it occurred alone. A significant increase in the length of roots of *T. rotundifolia* (29.25 cm) was recorded when *C. odorata* and *T. rotundifolia* occurred at a ratio of 5:1 but this decreased when *T. rotundifolia* density increased with a corresponding reduction in the density of *C. odorata.*

Table 3. Growth parameters of *T. rotundifolia* and *C. odorata* under different levels of interspecific competition

Growth param.	Plant species	Plant mixture (ratio)						
		6CR:0TR	5CR:1TR	4CR:2TR	3CR:3TR	2CR:4TR	1CR:5TR	0CR:6TR
Height	CR	36.44±2.96[d]	35.05±2.74[c]	34.43±3.03[b]	40.08±2.88[e]	33.25±1.98[a]	33.00±2.38[a]	0.00
(cm)	TR	0.00	106.75±15.32[f]	53.81±7.13[d]	68.83±9.22[e]	40.27±2.10[a]	49.36±8.62[c]	45.68±3.83[b]
Stem girth	CR	1.80±0.05[d]	1.63±0.05[c]	1.58±0.04[b]	1.64±0.15[c]	1.59±0.08[b]	1.48±0.09[a]	0.00
(cm)	TR	0.00	3.80±0.20[f]	3.01±0.15[e]	2.87±0.15[d]	2.41±0.09[b]	2.30±0.09[a]	2.58±0.14[c]
No of	CR	16.58±0.85[f]	13.20±1.47[d]	11.06±0.77[b]	14.25±1.29[e]	12.00±0.20[c]	9.00±1.91[a]	0.00
leaves	TR	0.00	21.75±3.12[e]	21.13±0.55[d]	26.42±12.21[f]	17.81±0.34[c]	16.60±4.87[b]	10.83±0.24[a]
Leaf area	CD	33.04±2.81[e]	23.79±1.88[c]	23.22±1.08[c]	27.52±17.56[d]	17.58±1.70[b]	16.39±1.71[a]	0.00
(cm^2)	TR	0.00	220.28±43.74[f]	92.70±18.42[b]	138.81±67.29[e]	98.63±6.12[d]	93.52±30.43[c]	58.43±5.98[a]

Where CR= *Chromolaena odorata,* TR= *Tithonia rotundifolia.*

Values are mean ± standard error for 5 replicates. Means with similar alphabets in superscript on the same row are not significantly different from each other at p≥0.05 (Duncan Multiple Range test).

The root to shoot ratio (R:S) of *C. odorata* decreased with increasing density of *T. rotundifolia* (Table 4). R:S of *C. odorata* was highest (0.20) in the absence of *T. rotundifolia* (6:0). This value was however not significantly different from the R:S of *C. odorata* when the ratio of the density of the two plants were 5:1 and 4:2 but differed significantly when the densities of *C. odorata* to *T. rotundifolia* were 3:3 (0.13), 2:4 (0.14) and 1:5 (0.15). *T. rotundifolia* equally had high R:S (0.49) in the absence of *C. odorata* which differed significantly from all other combination levels of the two plants. At high density of *C. odorata*, the R:S of *T. rotundifolia* was significantly low; 5CR:1TR (0.21) and 4CR:2TR (0.19) compared to R:S obtained at 2CR:4TR (0.42).

Table 4. Root growth of *C. odorata* and *T. rotundifolia* under different levels of interspecific competition

Plant mixture (ratio)	Number of roots		Root length (cm)		Root: shoot ratio	
	CR	TR	CR	TR	CR	TR
6CR:0TR	9.33±1.02[d]	0.00	15.08±1.02[d]	0.00	0.20±0.11[b]	0.00
5CR:1TR	6.00±1.15[c]	11.90±0.55[b]	11.31±1.20[c]	29.25±2.80[c]	0.18±0.09[b]	0.21±0.09[a]
4CR:2TR	4.56±0.16[a]	11.00±1.08[a]	10.04±1.47[b]	23.13±2.73[b]	0.18±0.09[b]	0.19±0.08[a]
3CR:3TR	5.25±0.08[b]	14.75±0.55[c]	9.64±1.50[b]	22.15±1.69[b]	0.13±0.07[a]	0.25±0.09a
2CR:4TR	5.13±0.97[b]	11.56±1.16[b]	7.53±1.32[a]	18.93±2.09[ab]	0.14±0.08[a]	0.42±0.15[bc]
1CR:5TR	5.25±1.03[b]	11.90±0.55[b]	9.10±1.04[b]	15.49±0.63[a]	0.15±0.09[a]	0.38±0.08[b]
6TR:0CR	0.00	10.83±0.44[a]	0.00	16.23±1.51[a]	0.00	0.49±0.14[c]

Key: CR= *Chromolaena odorata,* TR= *Tithonia rotundifolia.*

Values are mean ± standard error for 5 replicates. Means with similar alphabets in superscript on the same column are not significantly different from each other at p≥0.05 (Duncan Multiple Range test).

The total fresh mass (6.39 g) and dry mass (1.75 g) of *C. odorata* were significantly higher in the absence of *T. rotundifolia* (ratio of 6:0) than in its presence as shown in Table 5. The fresh and dry biomass of *C. odorata* was significantly reduced when grown with *T. rotundifolia* compared to its monoculture. In contrast, *T. rotundifolia* in mixed culture with *C. odorata* (5CR:1TR) had high fresh (117.16 g) and dry (28.20 g) biomass which were significantly higher than the fresh (18.94 g) and dry (4.81 g) biomass of *T. rotundifolia* grown in monoculture (0CR:6TR).

Table 5. Fresh and dry mass, relative growth rate and moisture content of *C. odorata* and *T. rotundifolia* grown under interspecific competition

Plant mixture (ratio)	Total fresh mass (g)		Total dry mass (g)		Relative growth rate (mg/g)		Moisture content (%)	
	CR	TR	CR	TR	CR	TR	CR	TR
6CR:0TR	6.39±1.12^{b}	0.00	1.75±0.45^{b}	0.00	0.024±0.002^{b}	0.00	72.57±10.98^{a}	0.00
5CR:1TR	3.46±0.13^{a}	117.16±20.24^{b}	0.83±0.09^{a}	28.20±9.00a	0.017±0.001^{a}	0.032±0.004^{b}	76.15±11.01^{a}	75.93±11.00^{a}
4CR:2TR	3.50±0.11^{a}	108.72±22.28^{b}	0.92±0.08^{a}	23.92±8.12a	0.017±0.001^{a}	0.029±0.002^{b}	73.02±10.88a	75.71±10.89^{a}
3CR:3TR	3.78±0.14^{a}	105.28±22.81^{b}	0.97±0.10^{a}	25.41±8.44a	0.018±0.001^{a}	0.031±0.004^{b}	74.94±10.89^{a}	75.89±11.00^{a}
2CR:4TR	4.00±0.19^{a}	25.64±9.00^{a}	0.89±0.06^{a}	5.51±0.33b	0.019±0.001^{a}	0.014±0.001^{a}	77.75±10.99^{a}	78.51±11.47^{a}
1CR:5TR	3.92±0.15^{a}	21.62±9.18^{a}	1.01±0.41^{a}	5.13±0.35b	0.018±0.001^{a}	0.012±0.001^{a}	74.50±9.35^{a}	76.27±11.23^{a}
6TR:0CR	0.00	18.94±8.09^{a}	0.00	4.81±0.22^{b}	0.00	0.010±0.001^{a}	0.00	74.60±10.54^{a}

Key: CR= *Chromolaena odorata,* TR= *Tithonia rotundifolia.*

Values are mean ± standard error for 5 replicates. Means with similar alphabets in superscript on the same column are not significantly different from each other at $p \geq 0.05$ (Duncan Multiple Range test)

Discussion

In the study, herbaceous plants, grasses and few shrubby species were found in the above ground vegetation of the invaded and uninvaded plots. The species richness of the above ground vegetation of the uninvaded plots were higher than those of the invaded plots across the plots covered in the study. The low richness of the weedy flora on the invaded plots can be explained by the fact that the vegetation cover in these plots consisted of monoculture stand of *T. rotundifolia* which provided vegetation cover with minimal open spaces for the survival of other plant species. In this situation, other weedy species could not have thrived. Many families contributed to the weedy species to the flora of the uninvaded plots. The prominent families in this study include the Fabaceae, Poaceae, Asteraceae, Rubiaceae, Amaranthaceae, Malvaceae, and Solanaceae in a diminishing order of importance. On the other hand, the invaded plots had a total of six families contributing to the weed flora with the Poaceae, Fabaceae and Euphorbiaceae listed as the major ones.

The recruitment data from the seed bank indicated a considerably large number of families making contribution to the seed bank of the invaded plots. While 14 families contributed plant species at the 0-15cm depths, 13 families were recorded at the 15-30 cm depth. The dominant plant family on the standing vegetation i.e., the Poaceae also made the highest contribution of seedlings to this soil seed bank. The Poaceae also dominated the seed bank of the uninvaded plots. Similar observation was reported by De Andrade and Miranda (2014) that Poaceae (64%) are often the most abundant species in the soil seed bank following fire disturbance in savanna ecosystem. The absence of tree species in the standing vegetation of the plots could also account for their absence in the soil seed bank. The high density of herbaceous seeds in the seed bank may be related to species traits where an earlier study had reported that herbaceous seeds remain viable for a longer period of time in the soil than other seed types (Ghersa and Martinez-Ghersa, 2000; Wang *et al*., 2009).

The result from this study shows that *T. rotundifolia* was either not found richly or totally absent in the seed bank of most of the invaded plots, though it was found in numerous populations in the standing vegetation. Its absence from the seed bank may be as a result of rapid seedling emergence from the soil which will likely promote its establishment and spread (invasion) in a new environment. This result has shown that formation of a large or persistent seed bank may not be essential for successful invasion in a new environment as pointed out by Gioria and Pyšek (2016). Contrarywise, many dominant plant species in the seed bank were absent in the above ground vegetation. Notable examples from the invaded plots are *Oldenlandia corymbosa* and *Mariscus alternifolius*. Although species composition in the above-ground and seed bank recruitments are often related such that the seed bank allows plant species that are lost from the vegetation to be re-established (Bakker *et al*., 1996), a low similarity was observed between the species composition of the seed bank and above-ground vegetation on the invaded and uninvaded plots in this study.

This study has also shown that the negative effect of competition was more pronounced on *C. odorata* compared to *T. rotundifolia* as evident in their growth parameters. A significant reduction in the above and below ground growth parameters of *C. odorata* was observed while the growth of *T. rotundifolia* was facilitated when in interspecific competition with *C. odorata* as against when in monoculture. The possession of higher growth by *T. rotundifolia* than *C. odorata* increased its chance of high productivity which may confer advantage on its invasive potential. The ability of *T. rotundifolia* to produce larger leaf surface area when in competition with *C. odorata* must have given it better photosynthetic ability for more rapid growth and better canopy layer to suppress growth of *C. odorata*. The improved root system of *T. rotundifolia* might have been responsible for better competition for water and nutrient absorption than *C. odorata*.

Increased density of the two plants when in mixed culture caused significant reduction on the root/shoot ratio of one another compared to when grown separately in monoculture. The study reported increased in the biomass of *T. rotundifolia* when in mixed culture contrary to the reduced biomass of C. odorata. At monoculture stand of *C. odorata*, the growth was better than when in competition with *T. rotundifolia*. In the presence of high density of *C. odorata*, the growth *T. rotundifolia* was significantly improved over when in monoculture stands and/or reduce density of *C. odorata*. This must have accounted for the gradual decrease in the population of *C. odorata* with rapid invasion of *T. rotundifolia* currently being observed in fallow land areas previously occupied by the former.

Conclusions

The presence of *T. rotundifolia* affected the richness and relative abundance of other plant species in the environment. The general paucity of weedy species contributing to the above flora on the invaded plots can be explained by the direct effect of *T. rotundifolia* mono clonal stand disrupting the ability of other weedy species to germinate therefore their dominance in the seed bank. It is likely that many plants will be driven to extinction if the invasion by *T. rotundifolia* continually persist since native species present in the soil seed bank are unable to germinate and maybe exposed to predation or decomposition in the soil. *T. rotundifolia* has some adaptations for competitive advantage over *C. odorata* and other plant species in the study area. This was through rapid seedling emergence after seed set; more rapid root growth for better water and nutrient uptake; and formation of canopy cover to suppress the growth of *C. odorata*.

Authors' Contributions

Conceptualization: YIB and OK; Funding acquisition: all authors; Data curation: ROA and ODF; Formal analysis: All authors; Writing - review and editing: YIB and OK.

All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

Acknowledgements

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

References

Adebowale A, Olorode O (2005). An overview of the invasive potential of Tithonia species (Asteraceae) in Nigeria. Science Focus 10(3):65-69.

Bakker JP, Poschlod P, Strykstra RJ, Bekker RM, Thompson K (1996). Seed banks and dispersal: important topics in restoration ecology. Acta Botanica Neerlandica 45:461-490.

Chao A, Chazdon RL, Colwell RK, Shen TJ (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters 8(2):148-159. *https://doi.org/10.1111/j.1461-0248.2004.00707.x*

De Andrade LAZ, Miranda HS (2014). The dynamics of the soil seed bank after a fire event in a woody savanna in central Brazil. Plant Ecology 215:1199-209. *https://doi.org/10.1007/s11258-014-0378-z*

Ghersa CM, Martinez-Ghersa MA (2000). Ecological correlates of weed seed size and persistence in the soil under different tilling systems: implications for weed management. Field Crops Research 67:141-148. *https://doi.org/10.1016/S0378-4290(00)00089-7*

Gioria M, Pyšek P (2016) The legacy of plant invasions: changes in the soil seed bank of invaded plant communities. Bioscience 66:40-53. *https://doi.org/10.1093/biosci/biv165*

Gioria M, Carta A, Baskin C, Dawson W, Essl F, Kreft H, … Pyšek P (2021). Persistent soil seed banks promote naturalisation and invasiveness in flowering plants. Ecology Letters 24(8):1655-1667. *https://doi.org/10.1111/ele.13783*

Hoffmann W, Poorter H (2002). Avoiding bias in calculations of relative growth rate. Annals Of Botany 90(1):37-42. *https://doi.org/10.1093/aob/mcf140*

Joshi J, Vrieling K (2005). The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. Ecology Letters 8(7):704-714. *https://doi.org/10.1111/j.1461-0248.2005.00769.x*

Kekere O, Babatunde AF, Akinbuwa O (2020). Assessment of growth, yield and fruit nutritional composition of tomato and sweet pepper irrigated with abattoir wastewater. Science Letters 8(2):69-77.

Larson JE, Funk JL (2016) Regeneration: An overlooked aspect of trait-based plant community assembly models. Journal of Ecology 104:1284-1298. *https://doi.org/10.1111/1365-2745.12613*

Thompson K, Grime JP (1979). Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67:898-921. *https://doi.org/10.2307/2259220*

Uyi OO, Igbinosa IB (2013) The status of *Chromolaena odorata* and its biocontrol in West Africa. In: Zachariades C, Strathie LW, Day MD, Muniappan R (Eds). Proceedings of the eighth international workshop on biological control and management of *Chromolaena odorata* and other Eupatorieae, Nairobi. ARC-PPRI, Pretoria, 1-2 November 2010, pp 86-98

Wang J, Ren H, Yang L, Li D, Guo Q (2009). Soil seed banks in four 22-year-old plantations in South China: Implications for restoration. Forest Ecology and Management 258:2000-2006. *https://doi.org/10.1016/j.foreco.2009.07.049*

Zhang L, Li Y, Huang J, Liu J, Liu X (20190. Evaluation of the short-term and long-term performance of biological invasion management in the China-Myanmar border region. Journal of Environmental Management 240:1-8. *https://doi.org/10.1016/j.jenvman.2019.03.061*