

Diversity of coevolved weeds in smallholder maize fields of Mexico and Zimbabwe

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Abstract Theory and empirical data suggest the areas of origin of a crop to be the general area of origin of its coevolved weeds. These longer evolved weeds would have an advantage over species with a shorter evolutionary time and migrate more successfully. We seek to identify patterns by comparing two regions with a shared crop, similar physiographic traits, but little direct contact, one of which is the area of origin of the crop. We compared the diversity of the maize weed flora and its edible components between two rural villages each of Oaxaca, Mexico, and Honde Valley, Zimbabwe, using vegetation sampling, interviews and participatory observation. The Mexican fields had higher species richness and diversity than the Zimbabwean ones. Species richness and densities were higher in the villages that receive more rainfall. Mexican fields had a mainly native weed flora with almost 80% American species and very few of African origin, whereas Zimbabwe had 32% of American and 50% of African origin. The regions shared seven American species and one of African origin. American/Mesoamerican agrestal weeds appear to be more successful in maize. Subsistence farmers in both study areas consumed about 19 edible weed species of which four were common to all villages. Our results also suggest that the presence of 3–4 species of edible weeds per field may be a general pattern in the maize-based systems, and that people not necessarily want or need more, so usefulness—at least as an edible plant—would have a limited influence on migration success.

Keywords Weed diversity · Weed evolution · Biogeography · Edible weeds

Introduction

Weeds are plants that grow entirely or predominantly in habitats disturbed by humans without being deliberately cultivated (Baker 1974). Another definition is plants that grow where they are not wanted. However, weeds, just like domesticated plants, are part of an

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experiment in rapid evolution: agrestals and other weeds may be quite distinct from the taxa they originated from. They have been exposed to natural selection, migration, hybridization and introgression in the unique ecosystem of the cultivated field, for just as long as their associated domesticated crops; many originated in this ecosystem by auto- and allo-ploidy and various hybridization mechanisms (Baker and Stebbins 1965; Baker 1974; Hairston et al. 2005; Vibrans 2002).

The evolutionary history of weeds may be relevant to a modern problem: that of exotic invasive plants. Various explanations have been proposed for the notorious differences in proportions of exotic plants in different regional floras, and the differential success of introduced species. Explanations include the level of purposeful introduction and acclimatation (and the related propagule pressure), enemy escape, and diversity of the native vegetation. However, the recent evolutionary history of the taxa, the selection pressures under which weeds have evolved and thus their differing levels of preadaptation has been considered only very occasionally, mainly in Europe, where the weed flora is well known (Ellenberg 1996). Also, most research on invasive agricultural weeds is conducted in modern production systems that are far removed from the type of systems in which most weeds evolved originally.

As Gray's 1879 hypothesis predicts, some of the ancient areas of origin of agriculture appear to be centers of origins for weeds, and do have lower proportions of exotic weeds, though this is a poorly-studied subject (Dafni and Heller 1980; Vibrans 2002; Zohary 1973). Regions that have been recently transformed by agriculture, such as Canada, USA, Argentina and Australia, tend to have the highest proportions of naturalized exotic species, and most problems with exotic invasive species. There are also indications that niches opened up by new disturbance types will be filled up by preadapted suites of plants (Moles et al. 2008): witness the "Africanization" of the neotropical grasslands with species coevolved with the large mammals of Africa, after the introduction of cattle ranching (Parsons 1970).

Weeds are generally considered to interfere negatively with agriculture and a large number of studies are dedicated to the development and application of technologies geared towards the eradication of weeds and their negative effects on crops (Chivinge 1990; Chatizwa and Vorage 2000; Gatsi et al. 2001; Rambakudzibga et al. 2002; Musambasi et al. 2002). However, not all weeds are detrimental. Some weeds are 'friendly' (Kunkel 1981) or useful elements in the agricultural ecosystem. They provide food, medicines and fodder (Espinosa-García and Díaz-Pérez 1996; Vieyra-Odilon and Vibrans 2001), they are important in the prevention of soil erosion (Chacón and Gliessman 1982; Calderón de Rzedowski and Rzedowski 2004), can be used as biopesticides (Hillocks 1998) and may also play a role in controlling insect pests (Peñagos et al. 2003). According to Marshall et al. (2003) weeds are important in supporting biodiversity within agroecosystems, due to their association with other organisms such as birds and insects.

The favourable properties of some weeds are appreciated by traditional agriculturalists as evidenced by the 'relaxed' weeding they practice (Altieri et al. 1987); many farmers actually sponsor beneficial weeds. In the Valley of Toluca, Mexico, maize weeds increased the economic value of the useful biomass by 50% on average, without reducing the overall yield of the main crop (Vieyra-Odilon and Vibrans 2001). The economic benefits are derived from the sale of edible weeds and the use of weeds as fodder. More than 20 edible 'weeds' are cultivated in Mexico (Díaz-Betancourt et al. 1999). So, it is necessary to consider usefulness of species in the analysis of migration patterns.

Mexico is a centre of origin and domestication of maize, *Zea mays* L. (Piperno and Flannery 2001). It has a mainly native weed flora (Vibrans 1998) and is the area of origin of

many tropical weeds. Maize was taken to Africa around 1500 and has now become Africa's dominant food crop (McCann 2005). As in Mexico, where the diet is based on maize consumption, the crop now forms the staple in Zimbabwe and is present in all meals; as a porridge for breakfast and as "sadza" (a thick version of the porridge) for lunch and supper. The weeds of maize are also an important part of the diet in both countries. They are considered a relish in Zimbabwe and 'quelites' (pot herbs) in Mexico.

In this paper, we compare species richness, species diversity, biogeographical components and abundance of weed vegetation from two regions with a traditional, weed tolerant agriculture, the same crop and relatively similar physiographic characteristics. The crop is native to one of the regions and was adopted in the other, substituting agronomically similar crops, mainly various types of millets. This study is part of a larger ethnobotanical investigation on wild-growing food plants; the fields studied were selected because informants had indicated that they were good sources for wild food plants. In addition, the number of food plants in each study plot was also compared.

We expect to find higher weed species diversity and richness, as well as a higher number of edible species in Mexico than in Zimbabwe because of the longer coevolution among maize, weeds and humans. Also, we expect more migration of maize weeds from America to Africa than in the opposite direction.

The study areas and crop management

The study sites were chosen based on:

1. Maize as the staple food, and its cultivation at subsistence levels in traditional, low-external-input systems.
2. Similar environmental physical factors in terms of soils (humic acrisols), average annual temperature (12–19°C), elevation (500–1900 m), latitude (16–18°) and annual rainfall (600 a 1,200 mm). These characteristics are described for the Land Unit G7 in which the Zimbabwean villages are located by Anderson et al. (1993). All study areas are in the mid-altitude tropics. Exactly equivalent sites could not be found, especially because soils tend to be neutral or alcaline in Mexico, whereas in Africa they are acid; when choosing the sites we emphasized soil type (humic acrisols) somewhat at the expense of other characteristics.

We selected two rural villages each for Mexico and Zimbabwe. Chipupuri and Maradzika are located in Honde Valley, Manicaland Province, Zimbabwe. In Mexico we worked in Santa Catarina Roatina (Roatina) and Villa Talea de Castro (Talea), both in the state of Oaxaca. The characteristics of each study site are shown in Table 1.

Field work was carried out during the November 2005–April 2006 rainy season in Zimbabwe. The crop field was generally prepared for planting by winter ploughing starting in August. Farmers with access to manure applied it at this stage. After the first significant rainfall in November, fields were ploughed again and planted. Most farmers used bought hybrid maize seed and planted it with some fertilizer. A top dressing of a fertilizer commonly known as Compound D was applied when the maize plants had reached knee height. Farmers used an ox-drawn cultivator for the first weeding and thereafter they weeded manually using hand-held hoes once or when necessary until the crop reached the reproductive stage. None of the farmers interviewed used herbicides. Two of the sampled maize fields in Maradzika were only weeded once because of labour shortages.

In Mexico, field work was done during the 2006 rainy season (May–October). In Talea field preparation began soon after the previous harvest by clearing the field of overgrown

Table 1 Environmental characteristics of the study sites

	Oaxaca, Mexico	Talea	Manicaland, Zimbabwe
	Roatina	Roatina	Chipupuri
Altitude ^a	1,789 m Maize fields were sampled at altitudes between 1,650 and 1,860 m	1,600 m Maize fields were sampled at altitudes between 1,000 and 1,750 m	952 m Maize fields were sampled at altitudes between 850 and 920 m
Latitude	16°16' N	17°22' N	18°33' S
Longitude	96°31' W	96°15' W	32°45' E
Mean annual precipitation	582.9 mm	1,640 mm (INEGI)	>1,000 mm (1,462 mm during November–April 2006) ^b
Rainy season	Summer (May–November)	20.6°C	Maradzika receives more rainfall than Chipupuri according to personal observations.
Mean annual temperature	19.9°C	Moist oak-pine forest and secondary vegetation used to shelter coffee plantations	Summer (November–April)
Vegetation	Pine forest and grasslands	Miombo woodland	19°C
Soil type	Entric Rigosols/humic acrisols	Humic acrisols	
Soil pH of sampled fields	7.13–8.57	4.9–6.5	4–4.6
Main crops	Grow maize, beans, squash, beans and squash	Maize, beans, squash, peanuts, coffee and sugar cane	Maize, beans, squash, peanuts, bananas, taro, mangos

^a Altitude measures were taken from the Municipal palace (Palacio Municipal) in Mexico and from the headman's residence in Zimbabwe. ^b Taken at Mukandze meteorological station, Zimbabwe. (Department of Meteorological Services, Bulawayo, Zimbabwe)

weeds and then the first ploughing. Farmers ploughed a second time in January/February and a third time a week or two before planting. Ploughing in Roatina was done twice; in February and before planting in May/June. Some farmers applied manure before planting and inorganic fertilizer 4–6 weeks after emergence. Fields were weeded 2–3 times until the crop had reached the reproductive stage. For the first weeding an animal-drawn (horse) cultivator was used; later weeds were pulled out manually or cut using machetes. Only one farmer used herbicides in his maize crop.

The farmers in Mexico plant local landraces of maize and they select seed from the previous crop. The maize varieties in Talea are planted according to differences in altitude and maturation period. For example, large white maize is planted on higher ground above the village where it is colder. This variety takes longer to mature, and is planted from late February and harvested in October. We worked only in the fields with early-maturing varieties (small white and small yellow maize) to make our data comparable to Roatina and Zimbabwe where there is a shorter growing season (3–4 months).

Methods

Interviews

We carried out age and sex group interviews using the local social structures (schools, churches and clubs). We interviewed eight groups in each community (males and females in the age classes 5–12, 13–19, 20–50 years and elders more than 50 years old). These interviews were aimed at creating floristic lists of edible wild plants from the combined effort of all group member, give insight into where plants are usually collected and general availability. All groups indicated the maize field as an important source of edible weeds. Thereafter ten families in each village were selected randomly and for willingness to participate in the study. Each of the selected families was asked to indicate one maize field they considered to be the best source of edible weeds which we used for sampling. Food diaries gave additional names of species used.

Sampling

The selected maize fields were sampled when at least half of the weed flora was flowering to facilitate specimen identification. This was usually after the fields had been weeded at least twice. A 5 m × 5 m quadrat was placed at least 2 m from the margins of the field and from the pathway to the field. All weeds present were listed using local or field names and percentage cover for each species was estimated visually using a modified Braun-Blanquet scale (Vieyra-Odilon and Vibrans 2001). Two 1 m² quadrats were then placed over a diagonal line of the 25 m² quadrat and individuals were counted for each species within the quadrat. Voucher specimens were collected and deposited in the Hortorio Herbarium (CHAPA) of the Colegio de Postgraduados, Texcoco, and in the National Herbarium of Zimbabwe (SRGH), Harare, for the Mexican and Zimbabwean species, respectively.

The Species diversity and richness program (Henderson and Seaby 1998) was used to calculate Fisher's alpha, Shannon's and Simpson's diversity indices for the weed flora using the number of individuals for each species found in the two 1 m² quadrats. Similarity between the sampling sites (25 m²) of Mexico and Zimbabwe was estimated using the Jaccard coefficient (NTSYSpc Version 2.10L) for species presence/absence data.

Results

Species richness and diversity

The maize weed flora in the study sites of Mexico consisted of 93 species (Roatina = 47 and Talea = 56 species) from 32 plant families (Appendix). The 70 species of weeds in Zimbabwe (Chipupuri = 42 and Maradzika = 50 species) were from 29 families. The sampling plots (25 m^2) each had between 13 and 15 species with standard deviations between ± 1.9 and 3.8 species in the four villages. The families with the largest number of species in both countries were Asteraceae, Poaceae, and Fabaceae. These three families combined had 40.4 and 35.2% of the species in Mexico and Zimbabwe, respectively.

Table 2 shows that weed diversity in the individual maize fields was generally higher in the maize fields of Mexico than in Zimbabwe according to Fisher's alpha, Shannon's and Simpson's inverse diversity indices. There were no significant differences between Talea and Roatina for Fisher's alpha ($P = 0.652$) and Simpson's D ($P = 0.312$) diversity measures, whereas Roatina had significantly higher measures for Shannon's index ($P = 0.027$). Contrary to our expectations, Maradzika consistently presented the lowest figures for these indices ($P < 0.002$). Maradzika had higher species richness (50 species) than either Chipupuri or Roatina and the highest weed densities. Maradzika tended to have a high number of unique species with low abundance and a few species with a large number of individuals. This may have influenced in the low diversity. It also presented the lowest evenness figures (0.23).

Biogeography

Eight species, *Amaranthus hybridus*, *Euphorbia heterophylla*, *Euphorbia hirta*, *Galinsoga parviflora*, *Lantana camara*, *Tridax procumbens* and *Xanthium strumarium* (native to America) and *Melinis repens* from Africa were found in the maize fields of both Mexico and Zimbabwe. Table 3 shows the 20 genera (representing 18.5% of 108 genera) occurring in both Mexico and Zimbabwe. Though they were not found directly in the sample plots, plants like *Cleome* sp. and *Triumfetta* sp. were also found growing around the maize fields in Mexico, increasing the similarity between the genera of weedy flora between Mexico and Zimbabwe.

Most of the maize field weed flora (80%) found in the sampling sites in Mexico were Mesoamerican or American elements while in Zimbabwe only 46% of the weeds had an African origin (Table 4). Over thirty percent of the weeds sampled in the Zimbabwe were American species, but only 3% of the Oaxaca species were native to Africa. American weeds may not have been introduced directly to Africa with maize but could have accompanied humans during activities like commerce and migration. Eurasian species played a small role in these tropical areas.

Eight weeds from Mexico and nine from Zimbabwe could not be identified to species level and were excluded from the distribution/origin statistic.

Similarity

According to the Jaccard coefficient for qualitative (presence/absence) data, species similarity between agrestal weeds of maize in Mexico and Zimbabwe was relatively low, with sampling sites sharing 1–2 species (*Amaranthus hybridus* and *Galinsoga parviflora*). Figure 1 shows that the Mexican villages clearly formed two distinct clusters, I and II separated by differences in soil pH and precipitation. It is drier in Roatina and the soil pH

Table 2 Weed diversity in the maize fields of Mexico and Zimbabwe

Field	Fisher's alpha			Shannon			Shannon evenness			Simpson's D		
	R	T	C	M	R	T	C	M	R	T	C	M
A	2.25	2.93	3.40	2.18	1.57	1.87	2.01	1.63	0.33	0.42	0.34	4.44
B	6.92	5.28	2.83	2.51	2.20	2.01	1.82	1.21	0.46	0.42	0.25	10.32
C	5.43	2.29	3.80	1.42	2.18	1.88	1.92	1.22	0.46	0.38	0.26	6.23
D	4.47	4.24	4.26	1.85	1.91	2.04	2.05	1.12	0.39	0.40	0.26	7.74
E	5.81	2.62	2.39	2.10	2.22	1.64	1.81	1.41	0.43	0.43	0.23	6.55
F	1.41	3.47	2.30	1.27	1.47	2.14	1.58	1.20	0.34	0.34	0.38	8.86
G	3.14	2.97	2.16	1.37	1.58	2.06	1.89	1.30	0.31	0.45	0.33	4.36
H	2.94	2.92	2.53	3.82	1.78	2.11	1.85	2.32	0.37	0.44	0.39	0.49
I	4.52	3.54	1.81	2.54	1.84	2.02	1.33	1.68	0.39	0.42	0.28	0.23
J	4.72	2.89	3.28	2.79	1.82	1.87	1.71	1.89	0.38	0.39	0.36	0.40

R Roatina; T Talea; C Chipupuri; M Maradzika. The highest and lowest values for each index are italics

Table 3 Genera of weeds found in both Mexico and Zimbabwe

Genus	Mexico	Zimbabwe
<i>Ageratum</i>	<i>A. houstonianum</i>	<i>A. conyzoides</i>
<i>Amaranthus</i>	<i>A. hybridus</i>	<i>A. hybridus; A. thunbergii</i>
<i>Bidens</i>	<i>B. odorata; Bidens</i> sp.	<i>B. pilosa</i>
<i>Commelina</i>	<i>C. diffusa</i>	<i>C. africana; C. zambesica</i>
<i>Cyperus</i>	<i>C. hermaphroditus</i>	<i>C. distans; C. esculentus</i>
<i>Eleusine</i>	<i>E. indica</i>	<i>E. coracana</i> subsp. <i>africana</i> ; <i>E. coracana</i>
<i>Euphorbia</i>	<i>E. graminea; E. heterophylla; E. hirta; E. hyssopifolia</i>	<i>E. heterophylla; E. hirta</i>
<i>Galinsoga</i>	<i>G. parviflora</i>	<i>G. parviflora</i>
<i>Ipomoea</i>	<i>I. purpurea</i>	<i>I. plebeia</i>
<i>Kyllinga</i>	<i>K. pumila</i>	<i>K. intricata</i>
<i>Lantana</i>	<i>L. camara</i>	<i>L. camara</i>
<i>Melinis</i>	<i>M. repens</i>	<i>M. repens</i>
<i>Oxalis</i>	<i>O. corniculata; O. latifolia</i>	<i>O. semiloba</i> subsp. <i>semiloba</i>
<i>Richardia</i>	<i>R. scabra</i>	<i>R. brasiliensis</i>
<i>Setaria</i>	<i>S. geniculata</i>	<i>S. homonyma</i>
<i>Sida</i>	<i>S. haenkeana; S. rhombifolia</i>	<i>S. alba</i>
<i>Spermacoce</i>	<i>S. confusa; S. ocyoides</i>	<i>S. senensis</i>
<i>Tagetes</i>	<i>T. erecta; T. filifolia</i>	<i>T. minuta</i>
<i>Tridax</i>	<i>T. procumbens</i>	<i>T. procumbens</i>
<i>Xanthium</i>	<i>X. strumarium</i>	<i>X. strumarium</i>

ranged from 7.1 to 8.5; Talea is more humid, and soils are more acidic, ranging from 4.9 to 6.5. The similarity between Roatina and Talea was accounted for by nine species found in both areas: *Amaranthus hybridus*, *Bidens odorata*, *Castilleja arvensis*, *Galinsoga parviflora*, *Ipomoea purpurea*, *Melampodium divaricatum*, *Melampodium perfoliatum*, *Tagetes erecta*, and *Richardia scabra*. In Zimbabwe the dendrogram separated the maize field samples into four clusters. These were divided by soil pH as well as the age of the maize field. Cluster III is composed of maize fields from Chipupuri which had medium grained, sandy/clay/loamy and very strongly acid (pH 4) soils. The rest of the fields in this village formed a cluster (V) determined by the slightly acid (pH 5.5), medium grained sandy soils.

In Maradzika the maize fields separated into two groups mainly based on their relative age. Cluster IV is made up of fields that were established more than 5 years earlier whereas the fields in cluster VI had been cleared for cultivation in the previous 1–5 years. Cluster IV includes perennial species like *Albizia antunesiana*, *Brachystegia spiciformis*, *Dodonaea viscosa* and *Fadogia tetraquetra*. These species were found growing in the surrounding vegetation and some were left as stumps.

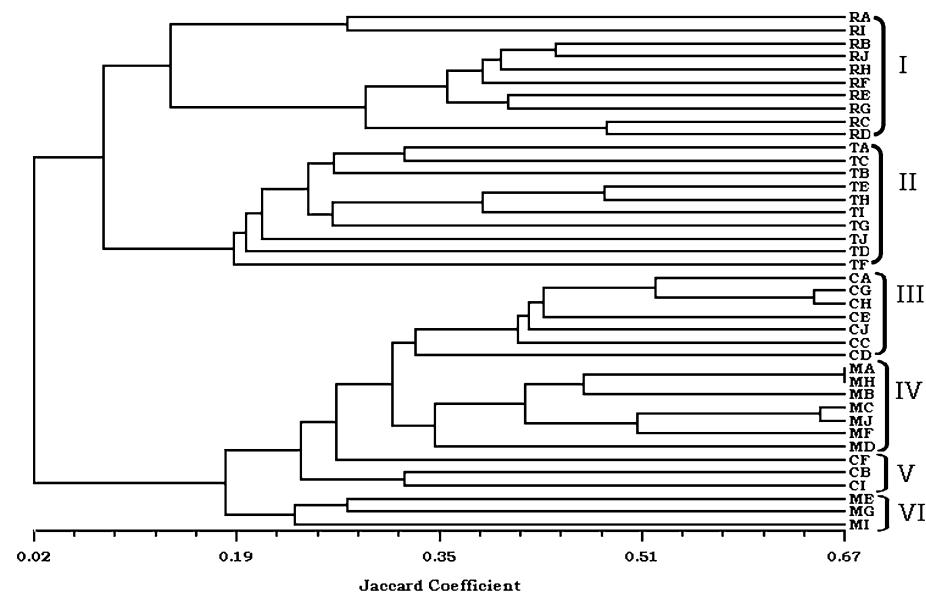
Density

Figure 2a shows the percentage cover estimates of all weeds in the 25 m² quadrats in the four villages. The wetter regions (Talea and Maradzika) had greater densities and cover estimates. Weed densities ranged from 6 to 34 plants m⁻² and from 19 to 100 plants m⁻² in Roatina and Talea and from 23 to 74 and 39 to 487 plants m⁻² in Chipupuri and Maradzika, respectively (Fig. 2b). The significantly high densities ($P = 0.05$) recorded for Maradzika resulted from two farmers failing to weed their fields for a second time due to labour shortages.

Table 4 Biogeographical origin of the weeds of maize in Mexico and Zimbabwe

Mexico			Zimbabwe		
Native region	No. of species	Proportion (%)	Native region	No. of species	Proportion (%)
America	55	59.1	Africa	8	11.4
Mesoamerica ^a	19	20.4	Tropical Africa ^b	24	34.3
Africa	3	3.2	America	23	32.9
Eurasia	5	5.4	Eurasia	–	–
Cosmopolitan/?	2	2.2	Cosmopolitan/?	5	7.1

^a Includes México; ^b Includes Zimbabwe; ? = Origin unknown



R=Roatina; T=talea; C=Chipupuri; M=Maradzika; A-J=Maize Field

Fig. 1 Species similarity in Roatina and Talea, Mexico and Chipupuri and Maradzika, Zimbabwe

Gathered edible weeds

Local people in both Mexico and Zimbabwe listed 19 species of weedy edible plants that they usually gathered from the maize fields. Four species, *Amaranthus hybridus*, *A. spinosus*, *Galinsoga parviflora* and *Sonchus oleraceus*, were mentioned in all four communities. Farmers weeded selectively to maintain the edible species, only removing them when densities were too high and threatened the main crop during the critical stages. Table 5 shows the diversity of edible weed species found in the maize fields of the four study areas. On average, there were 3–4 weed species considered edible in the 25 m² quadrats in all four villages.

In Mexico the most frequent edible weeds were *Galinsoga parviflora* which occurred in 75% of the fields sampled ($n = 20$), followed by *Amaranthus hybridus* and *Lopezia racemosa* that were present in half of the maize fields. The most frequently present edible weeds in Zimbabwe were *Bidens pilosa*, *Commelina zambesica* and *Galinsoga parviflora*, which occurred in 90, 85, and 65% of the fields, respectively. Except for *C. zambesica*

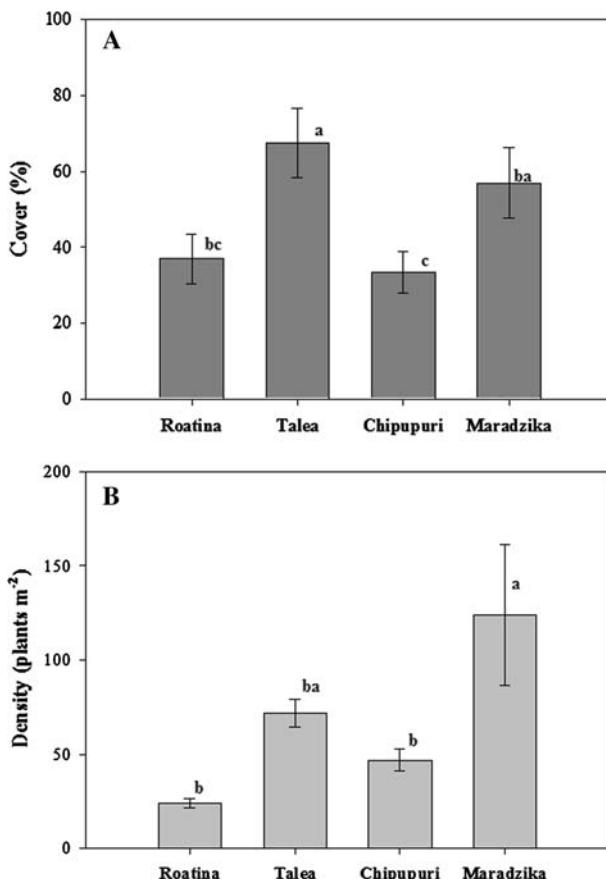


Fig. 2 Mean percentage cover estimates (A) and densities (B) (\pm SE) of maize weeds in Mexico and Zimbabwe. Bars with the same letter are not significantly different at $P = 0.05$ (LSD test)

Table 5 Edible weed species diversity in maize fields ($n = 10$)

	Roatina	Talea	Chipupuri	Maradzika
Total No. of weed species	47	56	42	51
Total No. of edible weed species	6	8	9	11
Proportion of edible species (%)	12.8	14.3	21.4	21.6
No. of edible weed species per plot \pm SE ^a	3.1 ± 0.46	4.1 ± 0.41	4.3 ± 0.4	4.4 ± 0.48
% cover of edible species \pm SE	1.1 ± 0.54	2.55 ± 0.47	2.08 ± 0.5	8.56 ± 1.8

^a standard error

(a famine food) in Zimbabwe and *L. racemosa* in Mexico, the most frequent species were also the most frequently consumed during the study periods in the four communities.

Discussion

The high proportion of Mesoamerican weeds in both maize weed floras—and the low proportion of African weeds in Oaxaca—supports the hypothesis of predisposition of longer

evolved weeds to migrate with their coevolved crop. The similarity in species and genera of weeds associated with maize between Mexico and Zimbabwe may be explained by preadaptation within taxonomic groups.

Total species richness in our study areas was comparatively low considering that we studied maize fields in rather weed tolerant environments. Most studies of agrestal weeds for a village area in Mexico cite more species than those found in this study (47, 56). This may be attributed to differences in the sampling effort. While we only sampled once in ten 25 m² plots during the maize growing season, others have collected weeds at least twice or continuously throughout the season. For example, Perdomo et al. (2004) documented 79 weeds in sugarcane in a small area in Morelos, Vieyra-Odilon and Vibrans (2001) found 74 species in a village of the Valley of Toluca, and Vibrans (1997) documented 88 agrestal weeds in a village in Tlaxcala, but these authors collected all the maize weeds they could find. There are no comparable data for Zimbabwe.

Species diversity is a community attribute that has not been frequently used in the evaluation of agrestal weeds. Most studies that have evaluated diversity in agrestal weeds have focused on the spatial and temporal variation in weed diversity as well as the effects of different management practices on weed species diversity (Perdomo et al. 2004). Studies on species diversity of weeds in the context of traditional peasant agriculture are uncommon. Our study areas had relatively high diversity indices, compared with other studies, especially in Talea with $H' = 3.08$. Hyvönen and Salonen (2002) and Tomita et al. cited by Perdomo et al. (2004) reported diversity values of 1.52 *Secale cereale* L. and between 1.0 and 1.4 in *Oryza sativa* L., respectively. Unpublished data in maize fields of Jalisco (Gamboa-Ruiz 2004) and Tlaxcala (González-Amaro 2008), respectively, document H' values of between 1.26–1.93 and 0.82–2.57. These measures are mostly influenced by the crop management practices practiced by the local farmers and by climate.

The edible components of the weed vegetation in maize fields are mostly used as green vegetables (potherbs, and relishes) to accompany the maize staple in both areas. This is an important practice as these plants provide vital micronutrients (Grivetti and Ogle 2000; Vieyra-Odilon and Vibrans 2001). Some have relatively high levels of lysine and thus increase the biological value of the staple (McGregor 1995). Moreover these resources have substantive economic value, either as food or as fodder (Vieyra-Odilon and Vibrans 2001).

Other studies in Mexico also indicate ranges of edible weed proportions similar to those reported in the present study. Vieyra-Odilon and Vibrans (2001) documented that 15% of agrestal weeds of maize were considered edible and consumed as potherbs while in Tlaxcala farmers consume about 20% of the weeds found in and around the maize crop (González-Amaro 2008). The abundance of edible wild plants in arable areas is also reported for other areas of Africa (Dovie et al. 2007; Keding et al. 2007). Ethnobotanical studies of wild food plants in Ethiopia, for example, indicated that 20% of the wild food plants consumed in the country are found in cultivated places (Asfaw and Tadesse 2001). In Kenya, the *Piik ap Oom* Ogiek, most commonly eat wild and weedy greens from gardens and maize fields (Marshall 2001). High and Shackleton (2000) report that in the Bushbuckridge region of South Africa, wild edible spinach-like vegetables are the most commonly found and used species (12 species out of 15) in home gardens. Modi et al. (2006) also reported that in KwaZulu Natal, South Africa wild leafy vegetables were comparatively more available in cropping fields than in the veld.

The proportions of edible weed components in our samples do not represent the total potential usefulness of the weed flora as a source of food because several species that are known food species were not deemed edible in the localities studied. The local people in Roatina and Talea, Mexico, did not include in their diet some species considered edible in

other regions. Some informants knew that *Anoda cristata* and *Malva parviflora*, for instance, are consumed in other Mexican states like Puebla but they had never tried them. *Lopezia racemosa* is used as a pot herb ('quelite') in Talea but is not considered edible in Roatina. Although edible species like *Portulaca oleracea* were not encountered in our sampling plots, it is a common weed in both areas, but is not consumed in the study communities of Zimbabwe, yet it is an important vegetable in other parts of Africa like Ethiopia (Asfaw and Tadesse 2001) and is even cultivated in Mexico (Linares and Bye 1992; Diaz-Betancourt et al. 1999). Similarly, *Bidens odorata* is a common weed that has potential as its leaves can be used as 'quelites' and to prepare tea (Gamboa-Ruiz 2004; Vibrans 2005). Furthermore, High and Shackleton (2000) document an average of 4.5 ± 2.15 herbs for each home garden in Bushbuckridge, South Africa, a number similar to our results. We suggest that a certain standard number of leafy green vegetables are considered sufficient by people to cover their dietary needs and desire for variation (Schwartz 2004), and new introductions would not necessarily be successful for this reason.

Conclusions

As expected, the Mexican weed communities had a higher proportion of native species, a richer weed flora and a higher diversity of the weed vegetation. Just as the American continent has contributed a large number of crops, including maize, to the African continent, it has also supplied a number of species that now form part of the weed flora. Our results support the hypothesis that weeds coevolve with crops, and that such coevolution leads to a higher probability of successful migration.

The comparison of the weed flora and the species used for food between the two countries that have had no direct contact showed some intriguing regularities that should be explored in a wider context:

- A relatively high proportion of shared genera between the weed floras suggest that there are predispositions for a weedy habit, in a similar way as some genera contain many domesticates.
- The number of species, densities and cover of agrestal weeds depend on the rainfall received during the season; they are higher in humid areas and rather similar in the areas with similar environments of the two continents.
- The number of edible weeds found in maize fields that were considered good sources of this type of vegetables was surprisingly similar, considering the contrasting cultural context. Three or four wild leafy vegetables from maize fields may provide sufficient choice for people to supplement local maize based diets. Usefulness as food then may not be a primary factor in plant migration.

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Appendix

See Tables 6, 7.

Table 6 Maize Weeds of Oaxaca, Mexico

Scientific name	Life form	Native region/distribution	Frequency
Amaranthaceae			
<i>Alternanthera lanceolata</i> (Benth.) Schinz ^a	Herb	C Mexico–Peru	3
<i>Amaranthus hybridus</i> L. ^a	Herb	America; tropical and temperate regions worldwide	10
<i>Gomphrena serrata</i> L.	Herb	Southern United States–Paraguay; naturalized elsewhere	3
Apiaceae			
<i>Spananthe paniculata</i> Jacq.	Herb	C Mexico–Bolivia	5
Asteraceae			
<i>Ageratum houstonianum</i> Mill.	Herb	Mexico–C America (Mesoamerica); naturalized in S USA and Australia	6
<i>Aldama dentata</i> Llave & Lex	Herb	C Mexico–Venezuela	6
<i>Ambrosia psilostachya</i> DC.	Herb	Canada–Mexico, naturalized elsewhere	1
<i>Bidens odorata</i> Cav.	Herb	Mexico and Guatemala (Mesoamerica); naturalized in S USA and South America	18
<i>Bidens</i> sp.	Herb	America	1
<i>Dysosmia papposa</i> (Vent.) Hitchc.	Herb	Canada–C America; South America	4
<i>Dysosmia sanguinea</i> (Klatt) Strother	Herb	Mexico–C America	2
<i>Galinsoga parviflora</i> Cav. ^a	Herb	Mesoamerica; widely naturalized elsewhere	15
<i>Jaegeria hirta</i> (Lag.) Less.	Herb	Mesoamerica; some areas in S America	4
<i>Melampodium divaricatum</i> (Rich.) DC.	Herb	Florida, Mexico–northern S America; secondary in Brazil and Myanmar	10
<i>Melampodium perfoliatum</i> (Cav.) Kunth	Herb	Mexico–C America; Cuba, California	6
<i>Sanvitalia procumbens</i> Lam.	Herb	Mexico–C America	4
<i>Sclerocarpus uniserialis</i> (Hook.) Benth. & Hook. f. ex Hemsl.	Herb	Texas, Mexico–C America	8
<i>Spilanthes alba</i> L'Hér. (= <i>Acmeilla alba</i> (L.) Hér.) J. K. Jansen	Herb	Mexico–S America; some populations in the Old World	1
<i>Tagetes erecta</i> L.	Herb	Mexico–C America	4
<i>Tagetes filifolia</i> Lag.	Herb	Mexico–northern S America	1
<i>Triaxac procumbens</i> L.	Herb	Mexico to tropical S America; naturalized in Old World tropics	1
<i>Xanthium strumarium</i> L.	Herb	N America, possibly Mexico; today worldwide	1
<i>Zinnia peruviana</i> (L.) L.	Herb	SW United States–S America	3
Brassicaceae			
<i>Lepidium virginicum</i> L. ^a	Herb	America, possibly North America; today worldwide	1

Table 6 continued

Scientific name	Life form	Native region/distribution	Frequency
Campanulaceae			
<i>Diastatea micrantha</i> (Kunth) McVaugh	Herb	Mexico–Bolivia	1
Caryophyllaceae			
<i>Drymocallis villosa</i> Schleid. & Cham.	Herb	Mexico–Perú, probable origin Mesoamerica	3
Commelinaceae			
<i>Commelinia diffusa</i> Burm. f.	Herb	Tropical & subtropical America	6
<i>Tripozandra purpurascens</i> (S. Schauer) Handl	Herb	Mexico–northern S America	3
Convolvulaceae			
<i>Ipomoea purpurea</i> (L.) Roth	Herb	America; today worldwide	3
Cyperaceae			
<i>Cyperus hermaphroditus</i> (Jacq.) Standl.	Herb	SW United States–S America	2
<i>Kyllinga pumila</i> Michx.	Herb	Temperate & tropical America, tropical Africa, origin uncertain.	1
Euphorbiaceae			
<i>Euphorbia hyssopifolia</i> L.	Herb	Mexico–S America; Old World tropics	1
<i>Euphorbia graminea</i> Jacq.	Herb	Tropical America; Florida, Hawaii, Oceania	1
<i>Euphorbia heterophylla</i> L.	Herb	S United States–S America; Old World tropics and subtropics	2
<i>Euphorbia hirta</i> L.	Herb	Tropical America; Oceania, Asia	2
Fabaceae			
<i>Crotalaria longirostrata</i> Hook. & Arn. ^a	Herb	Mexico–C America; Hawaii	1
<i>Crotalaria micans</i> Link	Shrub	Mexico–S America	1
<i>Crotalaria pumila</i> Ortega ^a	Herb	Mesoamerica (S USA to northern S America); Oceania	1
<i>Inga</i> sp. ^a	Tree	–	1
<i>Medicago polymorpha</i> L.	Herb	Eurasia; worldwide in temperate climates	1
<i>Mimosa pudica</i> L.	Herb	S America; today in tropics worldwide	3
Hamamelidaceae			
<i>Liquidambar styraciflua</i> L.	Tree	United States–C America	1
Lamiaceae			
<i>Hyptis atrorubens</i> Poit.	Herb	Mexico–Brazil and the Antilles; Africa	1
<i>Hyptis mutabilis</i> (Rich.) Briq.	Herb	Florida and Mexico–northern S America	3
<i>Marrubium vulgare</i> L.	Herb	Europe and adjoining areas; today worldwide in temperate and subtropical regions	2
<i>Sativa hypoleuca</i> M. Martens & Galeotti	Herb	Mexico–S America	2
<i>Salvia tiliifolia</i> Vahl ^a	Herb	S USA, Mexico–northern S America	8

Table 6 continued

Scientific name	Life form	Native region/distribution	Frequency
<i>Salvia</i> sp.	Herb	–	2
Lythraceae			
<i>Cuphea acquiptala</i> Cav.	Herb	Mexico–Guatemala & Honduras	1
Malvaceae			
<i>Anoda cristata</i> (L.) Schlttl.	Herb	Mesoamerica; today from USA to south America	4
<i>Malva parviflora</i> L.	Herb	Europe; widespread in temperate and subtropical regions	6
<i>Sida haenkeana</i> C. Presl	Herb	Mexico–Panama	6
<i>Sida rhombifolia</i> L.	Herb	Tropical and subtropical America; Old World tropics	2
Nyctaginaceae			
<i>Mirabilis jalapa</i> L.	Herb	Mexico–S America; secondary in some other regions	2
Onagraceae			
<i>Gaura coccinea</i> Pursh	Herb	Canada–Mexico	1
<i>Lopezia racemosa</i> Cav. ^a	Herb	Mexico–El Salvador	10
Oxalidaceae			
<i>Oxalis corniculata</i> L.	Herb	Unknown origin; possibly American; today worldwide	3
<i>Oxalis latifolia</i> Kunth	Herb	Mesoamerica; today from S USA–S America, naturalized in the Old World	2
Papaveraceae			
<i>Argemone ochroleuca</i> Sweet	Herb	Mesoamerica; naturalized in the tropics of the Old World	1
Phytolaccaceae			
<i>Phytolacca icosandra</i> L.	Herb	Mexico–S America & the Antilles; naturalized in some areas of Europe	1
Plantaginaceae			
<i>Plantago</i> sp.	Herb	–	1
Poaceae			
<i>Arthraxon quartianthus</i> (A. Rich.) Nash	Herb	Africa and Asia; USA to C America, Antilles	3
<i>Cenchrus echinatus</i> L.	Herb	S United States–S America ; widespread in tropics	2
<i>Digitaria sanguinalis</i> (L.) Scop.	Herb	Eurasia; widespread worldwide	2
<i>Eleusine indica</i> (L.) Gaertn.	Herb	Africa; widespread worldwide	2
<i>Eragrostis mexicana</i> (Hornem.) Link	Herb	Mexico; S America, Australia	2
<i>Heteropogon contortus</i> (L.) P. Beauv. ex Roem. & Schult.	Herb	America; Caribbean Islands and Old World Tropics	1
<i>Hilaria cenchroides</i> Kunth	Herb	Mexico to Guatemala	1
<i>Melinis repens</i> (Willd.) Zizka	Herb	Africa; tropics worldwide	1

Table 6 continued

Scientific name	Life form	Native region/distribution	Frequency
<i>Ophioglossum burmannii</i> (Retz.) P. Beauv.	Herb	Cosmopolitan, perhaps of Asian origin	2
<i>Paspalum humboldtianum</i> Flüggé	Herb	Mexico to S America	1
<i>Setaria geniculata</i> (Lam.) P. Beauv.	Herb	America; Old World tropics	2
Primulaceae			
<i>Anagallis arvensis</i> L.	Herb	Eurasia; widespread in temperate and subtropical regions	1
Pteridaceae			
<i>Pteridium aquilinum</i> (L.) Kuhn	Herb	Cosmopolitan	1
Ranunculaceae			
<i>Ranunculus perfoliatus</i> Kunth ex DC.	Herb	Mesoamerica (S USA to northern S America)	1
Rubiaceae			
<i>Borreria latifolia</i> (Aubl.) K. Schum.	Herb	Tropical America; invasive elsewhere	3
<i>Borreria ocytoides</i> (Burm. f.) DC. (= <i>Spermacoce ocytoides</i> Burm. f.)	Herb	Tropical Asia; Africa, Mexico–S America	2
<i>Crucea calocephala</i> DC.	Herb	Mesoamerica	3
<i>Mitracarpus hirtus</i> (L.) DC.	Herb	S US–Brazil & the Antilles; Old World tropics	5
<i>Ricardia scabra</i> L.	Herb	S United States–northern S America; Old World tropics	4
<i>Spermacoce confusa</i> Rendle ex Gillis	Herb	Mexico–Brazil and the Antilles; Hawaii and Africa	1
Scrophulariaceae			
<i>Castilleja arvensis</i> Schlehd. & Cham.	Herb	Mexico–S America; Hawaii and Oceania	2
Smilacaceae			
<i>Smitax</i> sp.	Herb	–	1
Solanaceae			
<i>Lycopersicon esculentum</i> Miller var. <i>leptophyllum</i> ^a	Herb	Mexico–S America	2
<i>Physalis peruviana</i> Mill.	Herb	Mexico	1
<i>Physalis philadelphica</i> Lam. ^a	Herb	SW United States–C America	7
<i>Solanum nigrum</i> L. Martens & Galeotti ^a	Herb	S United States–S America	1
Urticaceae			
<i>Pilea hyalina</i> Fenzl	Herb	Mexico–S America	3
Verbenaceae			
<i>Lantana camara</i> L.	Herb	S US–S America; in semiarid regions elsewhere	1
<i>Lippia</i> sp.	Shrub	–	1
<i>Verbena carolinina</i> L.	Herb	SW US–C America	1

^a Edible species; *Boldface*, considered native to Mexico; Frequency, number of times found in fields ($n = 20$); –, lacks information; C central; S south; SW south-western; unidentified species: 1 Fabaceae and 1 Chenopodiaceae

Table 7 Maize weeds of Honde valley, Zimbabwe

Scientific name	Life form	Native region/distribution	Frequency
Amaranthaceae			
<i>Amaranthus hybridus</i> L. ^a	Herb	Probably Mesoamerica; widespread in the tropics and temperate regions worldwide	5
<i>Amaranthus thunbergii</i> Moq. ^a	Herb	C, E & S Africa; introduced in USA, Europe and Australia	3
Anacardiaceae			
<i>Lannea edulis</i> (Sond.) Engl. ^a	Perennial herb	Tropical Africa	1
Annonaceae			
<i>Annona senegalensis</i> Pers. ^a	Shrub or tree	W, E & S Africa, Madagascar, Cape Verde	1
Apiaceae			
<i>Steganotenia araliacea</i> Hochst.	Shrub or tree	Tropical Africa	1
Asparagaceae			
<i>Asparagus plumosus</i> Baker	Herb	Southern Africa; naturalized in other continents	2
Asteraceae			
<i>Acanthospermum australe</i> (Loebl.) Kunze	Herb	S America; naturalized in North America, Europe, Africa, Asia, Oceania	5
<i>Acanthospermum hispidum</i> DC.	Herb	C–S America; widely naturalized in other continents	13
<i>Ageratum conyzoides</i> L.	Herb	Neotropics, probably Mesoamerica; today widespread in tropics and subtropics	15
<i>Bidens pilosa</i> L. ^a	Herb	Mesoamerica; widespread in tropics worldwide	18
Conyza sp.	Herb	South America	2
<i>Crassocephalum sarecobasis</i> (DC.) S.Moore	Herb	Ethiopia–S Africa	1
<i>Galinago parviflora</i> Cav. ^a	Herb	Mesoamerica; one of the most widespread weeds of tropical and temperate regions worldwide	13
Senecio pergamaceus Baker	Herb	Tanzania–Zimbabwe	3
<i>Tagetes minuta</i> L.	Herb	S America; widely naturalized in the tropics worldwide	10
<i>Tridax procumbens</i> L.	Herb	Mesoamerica and northern South America; naturalized in tropics elsewhere	3
<i>Xanthium strumarium</i> L.	Herb	N America; widespread in tropics and temperate regions worldwide	5
Boraginaceae			
<i>Trichodesma zeylanicum</i> (Burm.f.) R.Br.	Herb	Paleotropics (Africa, Asia, Australia)	1
Capparaceae			
<i>Cleome gynandra</i> L. ^a	Herb	Tropical Africa and Asia; naturalized in the Neotropics	2
<i>Cleome monophylla</i> L. ^a	Herb	Tropical & subtropical Africa; India	2
Caricaceae			
<i>Carica papaya</i> L. ^a	Tree	Tropical America	1

Table 7 continued

Scientific name	Life form	Native region/distribution	Frequency
Chrysobalanaceae			
<i>Parinari curatellifolia</i> Benth. ^a	Tree	Tropical Africa	1
Colchicaceae			
<i>Gloriosa superba</i> L.	Herb	Tropical Africa and Asia, naturalized elsewhere	1
Commelinaceae			
<i>Commelina africana</i> L. ^a	Herb	Tropical & S Africa	2
<i>Commelina zambesica</i> C.B. Clarke ^a	Herb	Africa	17
Convolvulaceae			
<i>Ipomoea plebeia</i> R. Br. ^a	Herb	Africa, South Asia and Oceania	5
Cucurbitaceae			
<i>Cucumis anguria</i> L. ^a	Herb	Southern Africa	1
Cyperaceae			
<i>Cyperus distans</i> L. f.	Herb	Origin unknown; pantropical	4
<i>Cyperus esculentus</i> L.	Herb	Variable species, pantropical	2
<i>Kyllinga brevifolia</i> Rott. subsp. <i>intricata</i> (Cherm.) J.P. Lebrun & Stork (= <i>Kyllinga intricata</i> Cherm.)	Herb	Origin unknown, pantropical	2
<i>Pycreus pelophilus</i> (Ridl.) C.B.Clarke	Herb	Tropical Africa	1
Euphorbiaceae			
<i>Euphorbia heterophylla</i> L.	Herb	Tropical America, exact origin obscure, possibly Mesoamerica; widely distributed in tropics worldwide	1
<i>Euphorbia hirta</i> L. (= <i>Chamaesyce hirta</i> (L.) Millsp.)	Herb	Tropical America, exact origin obscure, possibly Mesoamerica; widely distributed in tropics worldwide	1
<i>Uapaca kirkiana</i> Müll. Arg. ^a	Tree	Tropical Africa	1
Fabaceae			
<i>Albizia antunesiana</i> Harms	Tree	Congo-Botswana, Tanzania-Mozambique & Zimbabwe	1
<i>Brachystegia spiciformis</i> Benth.	Tree	Tropical Africa	1
<i>Desmodium tortuosum</i> (Sw.) DC.	Herb	Tropical America; today widespread in the tropics	1
<i>Leucaena leucocephala</i> (Lam.) de Wit	Shrub	Mesoamerica; today in tropics worldwide	1
<i>Mucuna pruriens</i> (L.) DC.	Liana	Tropical Africa and Asia; today worldwide	1
Lamiaceae			
<i>Leucas martinicensis</i> (Jacq.) R.Br.	Herb	Probably tropical America; common in Old World tropics	14
<i>Ocimum</i> sp.	Herb	—	5

Table 7 continued

Scientific name	Life form	Native region/distribution	Frequency
Malvaceae			
<i>Hibiscus cannabinus</i> L.	Herb	Africa ; widely naturalized elsewhere	6
<i>Sida alba</i> L. (= <i>Sida spinosa</i> L.)	Herb	Tropical America; widely naturalized elsewhere	6
<i>Hibiscus</i> sp.	Herb		1
Moraceae			
<i>Ficus</i> sp. ^a	Shrub	–	1
Myrtaceae			
<i>Psidium guajava</i> L. ^a	Tree	Tropical America, possibly Mesoamerica; widely naturalized elsewhere	1
Oxalidaceae			
<i>Biophytum petersianum</i> Klotzsch	Herb	Tropical Africa ; also in tropical Asia	1
<i>Oxalis semiloba</i> Sond. subsp. <i>semiloba</i> ^a	Herb	Tropical Africa	6
Poaceae			
<i>Eleusine coracana</i> (L.) Gaertn. subsp. <i>africana</i> (Kenn.-O'Byrne) Hilu & De Wet	Herb	Africa ; cultivated and sometimes escaped elsewhere	17
<i>Eleusine coracana</i> (L.) Gaertn. ^a	Herb	Africa ; naturalized in tropical Asia, America and some temperate regions	1
<i>Melinis repens</i> (Willd.) Zizka	Herb	Africa ; also in India	3
<i>Setaria homonyma</i> (Steud.) Chiov.	Herb	Tropical America; widespread elsewhere	7
<i>Sporobolus pyramidalis</i> P. Beauvo.	Herb		1
Rubiaceae			
<i>Fadogia tetraquetra</i> K. Krause ^a	Tree	Tropical Africa	3
<i>Richardia brasiliensis</i> Gomes	Herb	S America; today tropics worldwide	12
<i>Spermacoce senensis</i> (Klotzsch) Hiern	Herb	Tropical Africa	4
Sapindaceae			
<i>Dodoneea viscosa</i> Jacq.	Shrub	America; widely distributed in old world tropics	2
Scrophulariaceae			
<i>Striga asiatica</i> (L.) Kunze	Herb	Tropical S Africa, Madagascar, Arabia, across India to SE Asia and China ; occasionally elsewhere	2
Solanaceae			
<i>Nicandra physalodes</i> (L.) Gaertn.	Herb	Southern US–S America, Antilles, origin possibly Peru; old world tropics and temperate areas	5

Table 7 continued

Scientific name	Life form	Native region/distribution	Frequency
Tiliaceae			
<i>Corchorus olitorius</i> L. ^a	Herb	Tropical Africa and Asia	3
<i>Corchorus tridens</i> L. ^a	Herb	Tropical Africa and Asia, exact origin obscure; occasionally elsewhere	2
<i>Triumfetta pilosa</i> Roth ^a	Herb	Tropical Africa and Asia, occasionally elsewhere	3
<i>Triumfetta rhomboidea</i> Jacq. ^a	Herb	Probably Old World Tropics, today worldwide	4
Verbenaceae	Shrub	Southern US–S America, probably of Mesoamerica origin; today a world wide weed	1
<i>Lantana camara</i> L. ^a			

^a Edible species; *boldface* = considered native to Africa; frequency, number of times found in fields ($n = 20$); –, lacks information; C central; E, east; S, south; unidentified species; 4 Poaceae and 2 undetermined families

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