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Patterns of Folivory and Seed Ingestion by Gopher Tortoises (Gopherus polyphemus) in a Southeastern Pine Savanna

ROGER D. BIRKHEAD[1], CRAIG GUYER AND SHARON M. HERMANN
Department of Biological Sciences, Auburn University, Auburn, Alabama 36849

AND

WILLIAM K. MICHENER[2]
Joseph W. Jones Ecological Research Center, Newton, Georgia 39870

ABSTRACT.—This study documents the ingestion of leaves and seeds by gopher tortoises (*Gopherus polyphemus*) in a relatively intact pine savanna habitat. Fifty-three species of seeds were identified. Species richness of seeds ingested was highest during spring and fall and was lowest during summer. Grass seed and foliage were consumed consistently by tortoises throughout the year. Despite being found in only 12% of all scats, *Rubus* seed comprised half of all seeds recovered. Based on seeds in scats, tortoises ingested the fruits of plants in the same proportions in which the plants occurred immediately around active burrows. Although some kinds of leaves were less prevalent in scats than predicted by their availability near active tortoise burrows, this may have occurred because these leaves were digested and, therefore unrecognizable in scats. The role of the gopher tortoise as a generalist herbivore and an opportunistic frugivore was confirmed.

INTRODUCTION

Gopher tortoises (*Gopherus polyphemus*) are important grazers in upland pine savannahs of the southeastern United States where they may also be significant seed dispersal agents (Auffenberg, 1969; MacDonald and Mushinsky, 1988; Kaczor and Hartnett, 1990; Boglioli *et al.*, 2000). While several studies have documented folivory in gopher tortoises (MacDonald and Mushinsky, 1988; Birkhead, 2001; Carlson *et al.*, 2003), less is known about frugivory by this long-lived reptile (but *see* MacDonald and Mushinsky, 1988; Hayes *et al.*, 1989; Carlson *et al.*, 2003) and no study has summarized the types of fruits consumed by gopher tortoises during an entire season of activity. Because digestion is slow in gopher tortoises (Bjorndal, 1987; Birkhead, 2001) and individuals range over areas of 1–2 ha (Eubanks *et al.*, 2003), ingested seeds are likely to be moved beyond the vicinity of parent plants. Scats of gopher tortoises contain large intact plant parts, including seeds (MacDonald and Mushinsky, 1988), and seeds remain viable after ingestion (Birkhead, 2001; Carlson *et al.*, 2003). In addition, tortoises may concentrate seeds, package them in a nutrient-rich medium (the scat) and/or remove germination inhibitors. Therefore, the role played by gopher tortoises as a seed dispersal agent may affect the flora around their burrows and the surrounding habitat (Boglioli *et al.*, 2000).

[1] Corresponding author present address: Department of Biological Sciences, Auburn University, Auburn, Alabama 36849; Telephone: (334)844-4850; FAX: (334)844-9234; e-mail: birkhrd@mail.auburn.edu
[2] Present address: Long Term Ecological Research Network, UNM Department of Biology, Albuquerque 87106

In this study, folivory and frugivory by gopher tortoises is documented in a relatively pristine southeastern pine savanna. Numbers and types of seeds in scats and the seasons during which they were ingested are examined to document fruits in the diet of gopher tortoises. These data are compared with ingestion of foliage to infer the degree to which tortoises serve as frugivores and herbivores in this habitat.

METHODS

Our study was conducted at the Joseph W. Jones Ecological Research Center (JWJERC) at Ichauway Plantation, Baker County, in southwest Georgia. For maps and a detailed site description, *see* Drew *et al.* (1998). This preserve contains large areas of intact native groundcover managed with frequent fire (Atkinson *et al.*, 1996) and supports a large resident population of gopher tortoises (Boglioli, 1999; Ott, 1999; Boglioli *et al.*, 2000).

We collected scats opportunistically from tortoises captured during trapping efforts from 1996 to 2000. Although they were not collected continuously each year, these samples cover the major months of activity for gopher tortoises on this site: March through November (Eubanks *et al.*, 2003). Tortoises often defecated within minutes after capture and these scats were collected. We obtained additional samples from tortoises held overnight in the laboratory. All scats were placed in individual plastic bags, stored in a –40 C freezer, and later thawed, weighed and examined. Pellets were broken apart under running water in stacked 2 mm and 500 μm sieves. All material in the larger sieve was transferred to a large shallow pan and carefully separated with forceps. Coarse plant material (leaves and stems) was identified to the least inclusive taxon possible. Seeds were removed and set aside. All remaining fine material was poured through the coarse and fine sieves a second time. The contents of the fine sieve were placed in a small pan with approximately 5 mm of water, examined under a 10–40 power illuminated dissecting microscope, teased apart with needle probes and residual seeds extracted. All seeds were counted and identified to the least inclusive taxon (Nomenclature follows Radford *et al.*, 1968; Clewell, 1985; Drew *et al.*, 1998; Wunderlin, 1998). When possible, seed identification guides by Landers and Johnson (1976) and Martin and Barkley (1961) were used to categorize each seed type.

We recorded presence/absence data, by taxon, for leaves and seeds encountered in each tortoise scat. We categorized unidentified seeds into separate morphospecies, and all narrow leaves with parallel-veins were categorized as grass-like. Foliage of *Diodia* and *Richardia* were combined into a single category, as was foliage from *Centrocema* and *Clitoria*. Seeds of *Diodia* and *Richardia* also were pooled into one category. For some analyses, plants bearing seeds surrounded by thick, non-oily, edible pulp were categorized as being fleshy-fruited. For purposes of discussion, we defined large seeds as those $\geq$10 mm in maximum length.

A reference collection, created for all seeds found, was deposited in the JWJERC herbarium. The reference collection also included seeds collected directly from plants in the field and was used to help identify unknowns encountered in tortoise scats. All foliage was compared to specimens in the JWJERC Herbarium.

We conducted vegetation surveys at 16 active burrows randomly selected from 208 burrows that served as trap sites. At each selected burrow, a 1 × 1 m frame was placed 3 m directly in front of, behind and to each side of the burrow opening. Plants within the frame were identified and recorded; data from each burrow were pooled to serve as a measure of availability at burrows.

A one-way analysis of variance (SPSS) was used to test for seasonal changes in taxon richness of seeds in scat. Data from March and April were combined, as were those of October and November, because of low sample sizes. G-tests (Zar, 1999) were used to determine if counts of plant morphotypes found near active burrows were independent of

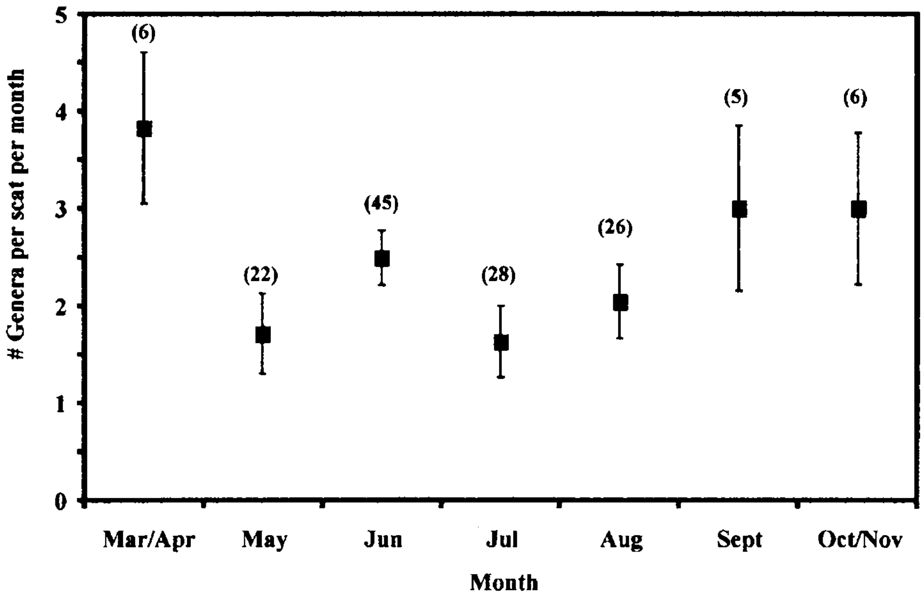

FIG. 1.—Average number (± 1 SE) of plant genera found per *Gopherus polyphemus* scat per month

those morphotypes found in scats. For G-tests, four morphotypes were used: legumes, fleshy fruits, grass-like and other (which includes broad-leafed forbs and woody vegetation such as *Cnidoscolous stimulosus*). Alpha was set at 0.05 for all analyses; 0.05 < alpha ≤ 0.10 was viewed to be marginally significant.

RESULTS

Twenty-seven families, at least 38 genera and an additional 15 unknown taxa were represented in the 11,459 seeds recovered from 138 tortoise scats (Appendix). The most common families (found in ≥5% of scats) were Gramineae, Rosaceae, Leguminosae, Turneraceae, Acanthaceae, Euphorbiaceae and Commelinaceae. The most common genera (found in ≥5% of scats) were: *Panicum, Rubus, Piriqueta, Dyschoristie, Stylosanthes, Paspalum, Tradescantia* and Unknown #12. *Rubus* seeds were found in 12.3% of scats sampled, but comprised more than half of the total number of seeds recovered.

There was a marginally significant difference among months in the number of taxa of seeds present in scats (F = 1.9, df = 6, P = 0.09); greater genera richness of seeds was found in Apr-May and Sept-Nov compared with Jun-Aug (Fig. 1). Seeds of grasses (principally *Panicum*) were common in scats throughout the active season of tortoises, however seeds of fleshy fruits (principally *Rubus, Physalis, Asimina* and *Licania*) occurred primarily in scats during August to November (Fig. 2).

There was a marginally significant difference between the morphotypes of plants found around burrows and the presence of those same morphotypes as foliage in scats (G-value = 6.42, df = 3, P = 0.09; Table 1). This pattern resulted from an under representation of foliage in the "other" category in scats relative to that available near active burrows. No difference was found between plant morphotypes found near burrows and the occurrence of seeds of these same morphotypes in scats (G-value = 1.49, df = 3, P = 0.68). An additional 13 taxa were found in scats but were not found in sample plots near active burrows.

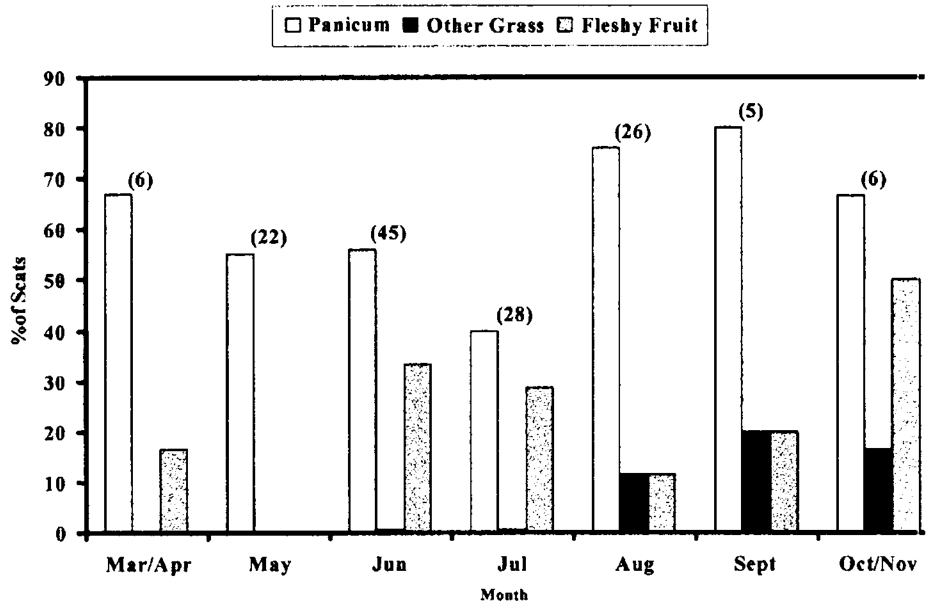

FIG. 2.—Presence of grass seeds (white bars = *Panicum* sp., black bars = other grasses) and fleshy fruited species (grey bars) in *Gopherus polyphemus* scat per month. Numbers above bars indicate number of scats examined each month

DISCUSSION

Tortoises at the JWJERC sampled foliage of grass-like, fleshy-fruited and leguminous plants in the same relative frequency that they occurred near active burrows. However, foliage of all other types of plants were underrepresented in scats, relative to their occurrence near active burrows. This difference most likely resulted from digestion of leaves and stems of these plants rather than avoidance of them as food items (Carlson *et al.*, 2003). This conclusion seems plausible because seeds of these morphotypes appear in scats with the same relative frequency that they are available near active burrows, an observation that suggests that tortoises sample vegetation indiscriminately. MacDonald and Mushinsky (1988) concluded that gopher tortoises were midway between being a specialist and a generalist and that plant apparentcy was not the determining factor for food selection.

At least 70 taxa of plants were ingested by gopher tortoises on the JWJERC. These include 32 taxa known to occur within 5 m of active burrows and 38 additional taxa likely eaten farther from the immediate vicinity of the burrow. These results confirm earlier findings by

TABLE 1.—Plant morphotypes found around active tortoise burrows and the frequency with which these genera are ingested as seed or foliage. Woody species that do not bear fleshy fruits (*Pinus* and *Quercus*) or that produce oily, thin-fleshed fruits (*Rhus*) were included in the "Other" category

Type	Near active burrows	Seed in scats	Foliage in scats
Grasslike	8	4	8
Fleshy Fruit	6	4	3
Legume	12	3	10
Other	27	9	6
Total	53	20	27

MacDonald and Mushinsky (1988) who found that gopher tortoises, while sampling plants in a non-random fashion, are generalist herbivores consuming at least 68 genera on a longleaf pine-turkey oak sandhill. At least 53 species of seeds were identified in gopher tortoise scats on JWJERC. Though very little literature exists, gopher tortoises may utilize a broader range of plants than any other frugivore/granivore within this system. The only comparable data for resident species exists for bobwhite quail for which 46 species of seed plants are important diet components (Martin, 1935). Feeding and seed ingestion/dispersal by gopher tortoises may help maintain the high plant diversity of the longleaf forests. The number of seeds ingested is also similar to the 51 different types of seeds ingested by spur-thighed tortoises (*Testudo graeca*) in a marsh-xerophytic shrubland ecotone in Spain (Cobo and Andreu, 1988) and the 28 species ingested by Aldabran Giant Tortoises (*Geochelone gigantea*) (Hnatuik, 1978). The high number of plant species ingested and potentially dispersed by tortoises is further evidence of their importance in many other types of ecosystems.

Overall, taxonomic diversity of seeds in gopher tortoise scats was higher in the spring and fall than in the summer. During May and July there was a slight depression in the number of genera of seeds found per scat, an observation that may indicate a preference by tortoises for fleshy fruits when they become available in summer. This result fits the model for an 'opportunistic' frugivore (McKey, 1975; Howe and Estabrook, 1977; Howe, 1986). Fleshy fruits are high in moisture and could be an important source of water for tortoises during summer months, a pattern observed in box turtles (*Terrapene carolina*; Klimstra and Newsome, 1960). Alternatively, seasonal patterns of seed diversity may mimic fruit availability. Growing-season fires reduce the number of seeds available for consumption during the late spring and early summer and most species of plant in these habitats produce seed in the late summer and fall (Carrington, 1997). Fire effects would explain the reduction of seed diversity in scats during summer, as well as the rise in the proportion of grass seed found in scats during the fall. If seeds ingested in fall over-winter in tortoise guts, diversity of seeds passed in spring could be high. This observation is supported by a scat collected in March that contained seeds from *Passiflora incarnata* and *Ambrosia* sp., plant species that produce fruit and seed only in late summer and early fall (Radford *et al.*, 1968).

Although rare in scat, large seeded plants may benefit from ingestion of their fruit by gopher tortoises. These reptiles defecate large seeds of *Asimina*, *Licania* and *Prunus* intact. Large seeds when compared to smaller seeds, are less likely to be ingested by frugivores, have fewer potential dispersers, and are more likely to be depredated (Janzen, 1971; Heithaus, 1981; Howe and Smallwood, 1982; Janzen, 1986; Venable and Brown, 1988). The large-seeded fruits that we observed in the diet of gopher tortoises also fit the syndrome of reptile-dispersed fruits in being aromatic, colorful and borne near the ground or dropped at maturity (Van der Pijl, 1982). These observations suggest that, although large-seeded taxa are infrequently observed in scats of gopher tortoises, these animals play an important role as dispersal agents for these plants in southeastern pine savannas.

Grass seeds (principally *Panicum*) were the most frequently ingested seeds observed in scats of tortoises at JWJERC. Such seeds were ingested throughout the active season of gopher tortoises. However, it is unlikely that grass seeds were deliberately targeted as a food source. More likely, these seeds were ingested via accidental consumption as a byproduct of folivory (Van der Pijl, 1982). Janzen (1984) proposed this as an adaptation of grasses for seed dispersal. Cobo and Andreu (1988) found a high proportion of Poaceae seed in tortoise scats and offered this as support for Janzen's idea.

Interestingly, the seed of wiregrass (*Aristida stricta*) were not observed from scats at the JWJERC. Wiregrass is an important component of southeastern pine savannas because it is highly flammable and is an indicator of intact native groundcover (Clewell, 1989; Hardin and White, 1989; Noss, 1989; Drew *et al.*, 1998). Auffenberg (1969) hypothesized that gopher tortoises disperse seeds of wiregrass. However tortoise dispersal of wiregrass seed does not appear to be the case at JWJERC and seems unlikely elsewhere because wiregrass seed matures on dehiscent stalks that are about 1 m tall, well above the height of most ground cover plants, and mature at a time period (Oct.–Dec.) when tortoises are relatively inactive. Therefore, *Aristida* seeds seem unlikely to be ingested accidentally.

The results of this study clarify the importance of gopher tortoises as folivores in southeastern pine savannas and elucidate the role of gopher tortoises as frugivores. Because gopher tortoises are long-lived, use multiple burrows within a site, occasionally move long distances (up to 1085 m in 2 d; Eubanks *et al.*, 2003), and construct or preferentially utilize burrows in areas of increased light (Aresco and Guyer, 1998; Boglioli *et al.*, 2000), they have the potential to be important seed dispersal agents (*see* also Carlson *et al.*, 2003). Additional work is needed to determine exact sites of scat deposition and seedling germination and survival under natural conditions.

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APPENDIX.—Plant species observed in vegetation surveys and tortoise scats from a southeastern longleaf pine-wiregrass savanna in southwest Georgia. In two cases *Centrocema/Clitoria* and *Diodia/Richardia,* pairs of species could not be distinguished and so were combined into a single category. Foliage of 10 grass-like species could not be distinguished from each other and so was combined into one large category that was present in 93% of all scats; these species are indicated by *. Types: F = fleshy, non-oily fruit, G = grass-like, L = legume, O = other forb or woody vegetation. N = total number of seeds recovered from all examined scats

				Scats				
						Seeds found in scats		
			% of Burrows	% with Foliage	% with Seed	N	Range	Average
Acanthaceae	*Dyschoriste oblongifolia*	O	100	1.41	6.52	38	1–14	4.2
	Ruellia caroliniensis	O	12.5	0	0	—	—	—
Aizoaceae	*Mollugo verticillata*	O	0	0	0.72	2	2	2
Anacardiaceae	*Rhus copallina*	O	50	0	0	—	—	—
Annonaceae	*Asimina longifolia*	F	18.75	20.42	2.17	35	5–19	11.7
Asclepiadaceae	*Asclepias* sp.	O	6.25	0	0.72	1	1	1
Cactaceae	*Opuntia humifusa*	F	0	2.11	0.72	1	1	1
Caryophyllaceae	*Stellaria media*	O	0	0	0.72	15	15	15
Chrysobalanaceae	*Licania michauxii*	F	37.5	1.41	1.45	7	3–4	3.5
Cistaceae	*Lechea* sp.	O	56.25	0	0	—	—	—
Commelinaceae	*Commelina erecta*	G	50	*	2.90	15	3–5	3.75
	Tradescantia ohioensis	G	0	*	5.07	65	1–30	9.3
Compositae	*Ambrosia* sp.	O	18.75	0	0.72	29	29	29
	Aster sp.	O	81.25	0	0	—	—	—
	Elephantopus sp.	O	25	0	0	—	—	—
	Eupatorium sp.	O	25	0	0	—	—	—
	Gaillardia aestivalis	O	0	0	2.17	20	2–41	6.7
	Gnapthalium sp.	O	12.5	0	0	—	—	—
	Liatris sp.	O	12.5	0	0	—	—	—
	Pityopsis graminifolia	G	87.5	*	0	—	—	—
	Rudbeckia sp.	O	6.25	0	0	—	—	—
	Vernonia angustifolia	O	6.25	0	0	—	—	—
Convolvulaceae	*Ipomea* sp.	O	6.25	0	0.72	3	3	3
	Stylisma patens	O	31.25	0	0	—	—	—
Cyperaceae	*Rhyncospora* sp.	G	43.75	*	0.72	1	1	1
	Scleria sp.	G	0	*	0.72	1	1	1
Ebenaceae	*Diospyros virginiana*	F	12.5	0	0	—	—	—
Ericaceae	*Gaylussacia dumosa*	F	18.75	0	0	—	—	—
	Vaccinium sp.	F	0	0.7	0	—	—	—
Euphorbiaceae	*Acaphyla gracilens*	O	0	0	2.90	215	1–117	26.9
	Cnidoscolus stimulosus	O	18.75	0	0	—	—	—
	Croton argyranthemus	O	81.25	0.7	0	—	—	—
	Tragia urens	O	68.75	0	2.90	12	1–7	2.4
Fagaceae	*Quercus* sp.	O	25	23.94	0	—	—	—
Gramineae	*Aristida stricta*	G	100	36.62	0	—	—	—
	Andropogon sp.	G	100	*	0	—	—	—
	Digitaria sp.	G	0	*	2.17	50	1–33	16.7
	Panicum sp.	G	87.5	*	45.65	1732	1–248	22.5
	Paspalum sp.	G	25	*	5.07	177	1–74	25.3
	Sporobolis sp.	G	25	*	0	—	—	—
Guttiferae	*Hypericum* sp.	O	6.25	0	0.72	1	1	1

APPENDIX.—Continued

			% of Burrows	Scats % with Foliage	% with Seed	Seeds found in scats N	Range	Average
Leguminosae	*Cassia* sp.	L	18.75	6.34	0	—	—	—
	Centrocema/Clitoria	L	75	29.58	0	—	—	—
	Crotalaria sp.	L	50	1.41	0	—	—	—
	Desmodium sp.	L	6.25	0	0	—	—	—
	Galactia sp.	L	31.25	0.7	0	—	—	—
	Lezpedeza sp.	L	50	17.61	0	—	—	—
	Rhyncosia reniformis	L	81.25	4.93	0	—	—	—
	Schrankia microphylla	L	56.25	25.35	0.72	1	1	1
	Stylosanthes biflora	L	37.5	0.7	6.52	77	1–34	7.7
	Strophostyles sp.	L	6.25	0	0	—	—	—
	Tephrosia sp.	L	62.5	19.72	0	—	—	—
	Zornia bracteata	L	18.75	1.41	2.17	11	1–8	3.7
Liliaceae	*Smilax* sp.	O	0	2.82	0	—	—	—
Onagraceae	*Oenothera* sp.	O	0	0	1.45	36	2–34	18
Oxalidaceae	*Oxalis* sp.	O	0	0.7	1.45	8	1–7	4
Passifloraceae	*Passiflora incarnata*	F	0	0	1.45	162	73–89	81
Pinaceae	*Pinus plaustris*	O	37.5	83.8	0	—	—	—
Plantaginaceae	*Plantago* sp.	O	0	0	2.17	605	1–277	86.4
Polygalaceae	*Polygala* sp.	O	6.25	0	0.72	27	27	27
Polygonaceae	*Erigonium tomentosum*	O	18.75	0	0	—	—	—
	Polygonum sp.	O	0	0	1.45	78	1–23	7.1
	Rumex sp.	O	0	0	0.72	1	1	1
Pteridaceae	*Pteridium aquilinum*	O	31.25	9.15	0	—	—	—
Rosaceae	*Crataegus* sp.	F	0	0	0.72	15	15	15
	Prunus angustifolia	F	0	0	1.45	5	1–4	2.5
	Prunus serotina	F	0	0	0.72	1	1	1
	Rubus sp.	F	75	16.9	12.32	6014	1–1281	334
Rubiaceae	*Diodia/Richardia* sp.	O	6.25	0	3.62	511	1–364	102
	Hedyotis sp.	O	12.5	0	0	—	—	—
Scrophulariaceae	*Veronica hederaefolia*	O	0	0	3.62	85	2–53	17
Solanaceae	*Physalis heterophylla*	F	18.75	0	3.62	70	5–39	14
Turneraceae	*Piriqueta caroliniana*	O	50	0.7	7.25	276	2–85	25.1
Unknown #1	—	—	—	—	1.45	664	8–656	332
Unknown # 2	—	—	—	—	0.72	2	2	2
Unknown # 6	—	—	—	—	3.62	83	1–48	16.6
Unknown # 7	—	—	—	—	1.45	3	1–2	1.5
Unknown # 11	—	—	—	—	2.17	11	1–9	3.67
Unknown # 12	—	—	—	—	5.07	186	1–114	26.6
Unknown # 13	—	—	—	—	3.62	21	1–15	4.2
Unknown # 14	—	—	—	—	0.72	1	1	1
Unknown # 15	—	—	—	—	0.72	1	1	1
Unknown # 17	—	—	—	—	1.45	10	2–8	5
Unknown # 20	—	—	—	—	4.34	68	2–40	11.3
Unknown # 21	—	—	—	—	0.72	6	6	6
Unknown # 22	—	—	—	—	0.72	1	1	1
Unknown # 23	—	—	—	—	0.72	1	1	1
Unknown # 24	—	—	—	—	0.72	3	3	3