Heterostyly in a tropical weed: the reproductive biology of the *Turnera ulmifolia* complex (Turneraceae)

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Turnera ulmifolia (Turneraceae) is a polymorphic complex native to the New World tropics which is composed of heterostylous and homostylous forms. The distylous varieties *elegans*, *intermedia*, and *surinamensis* exhibit the typical expression of heterostyly. Floral dimorphism is associated with a strong self-incompatibility system and size dimorphism of pollen. Approximately equal representation of floral morphs occurred in 24 out of 28 New World populations surveyed. In 9 out of 10 populations studied, there were no significant differences between the seed fecundity of floral forms. Populations of the homostylous variety *angustifolia* are self-compatible and produce monomorphic pollen.

In contrast to the majority of heterostylous species, some varieties of *T. ulmifolia* are ruderal weeds. Varieties *angustifolia*, *elegans*, and *intermedia* are also used as garden ornamentals, and man has played a major role in the expansion of their ranges. Weediness in *T. ulmifolia* is not associated with features commonly found in other weed species, such as self-compatibility, vigorous clonal propagation, and long-distance seed dispersal. However, the continuous year-round flowering of *T. ulmifolia* plants gives populations a high reproductive capacity. Seed dispersal is by ants which transport seeds relatively short distances. Local seed dispersal favors the establishment of dense populations and increases the likelihood of seed set. Hence the dispersal system of *T. ulmifolia* appears to be coadapted with the population requirements of the breeding system.

Introduction

Turnera ulmifolia L. (Turneraceae) is a herbaceous to woody perennial which is native throughout the Neotropics from Mexico to Argentina. It represents a polymorphic complex composed of white, cream, yellow, and blue flowered forms which can be either heterostylous or homostylous (Urban 1883).

Some varieties of *T. ulmifolia*, e.g., vars. *angustifolia*, *elegans*, and *intermedia*, are conspicuous elements of weed floras in both the New and Old World tropics. Populations occur on roadsides and in clearings and waste ground associated with human disturbance, but are rarely found as weeds of agricultural land or as components of undisturbed vegetation. Adventive populations of vars. *angustifolia* and *elegans* are reported as ruderal weeds in Mauritius, Madagascar, Seychelles, India, Sri Lanka, Malaysia, Indonesia, and Java (Lock 1904; Van Steenis 1931; Backer 1951; Brizicky 1961).

Attention has been drawn to the predominance of self-compatibility and particularly autogamy in weed species (Baker 1955, 1965; Stebbins 1957). Autogamy is considered to be adaptive to colonizing species by ensuring seed set regardless of population size and density (Baker 1955). Since heterostylous breeding systems are not generally associated with colonizing ability, a study of the reproductive biology of the heterostylous weed members of the *T. ulmifolia* complex was initiated.

The purpose of this paper is to describe the floral morphology and breeding systems of four varieties of *T. ulmifolia* and to document a survey of the reproductive biology of 30 populations occurring in Central and South America. In addition, some suggestions are made concerning the characters responsible for weediness in *T. ulmifolia*.

Materials and Methods

Urban (1883) recognized the polymorphic nature of *Turnera ulmifolia* and described 12 intergrading varieties within the complex. Later authors, working with adventive Asian populations, considered some varieties to be specifically distinct (Lock 1904; Van Steenis 1931; Backer 1951). Since no modern taxonomic revision of the complex is available (Brizicky 1961), Urban's treatment is followed in this paper. The varieties utilized in this study were *T. ulmifolia* vars. *angustifolia* Willd., *elegans* Urb., *intermedia* Urb., *surinamensis* Urb., and a hybrid form from Columbia which is intermediate between vars. *elegans* and *intermedia* in morphology (S. Barrett, unpublished data). Hereafter, varieties will be referred to by varietal names only and the Columbian form termed *elegans* × *intermedia*.

The locality, habitat, and varietal status of populations surveyed are presented in Table 1. Measurements of floral parts were obtained from a single flower from each of 30 individuals of each floral form in five populations. Style and stamen lengths were measured from the base of the style, and the shortest distance separating the stigmas and anthers within a flower was recorded. The equatorial axes of 100 dry pollen grains were measured for each floral form in five populations.

A controlled pollination program was undertaken in a pollinator-free glasshouse at the University of California, Berkeley, during 1973–1976. Plants used in the program were grown from seed obtained from open-pollinated plants in natural populations. The source and varietal status of these populations are presented in Table 2. Pollinations were made on emasculated flowers with the aid of forceps. Seed production resulting from various pollen–carpel combinations was compared using Student's t-test.

Thirty populations (see Table 1) were sampled in order to determine the representation of floral forms in each one. All flowering individuals in a population were scored for floral form. Where sample sizes were sufficient, equality of representation (isoplethy) was tested by chi-square analyses. The seed fecundity of floral forms in 10 populations was estimated. Capsules were harvested from the majority of individuals in each population and the number of seeds per capsule recorded.

Observations of flowering phenology and the occurrence of insect visitors to flowers of *T. ulmifolia* were made at the majority of populations. Detailed records of the foraging activity of *Exomalopsis* sp. (Anthophoridae) and skippers (Hesperiidae) were made at populations 16 and 28, respectively. Foraging records commenced at flower opening and continued for a 3-h period. A large number of insects was followed for a minimum of five interplant flights per individual. The style form and number of flowers visited on individual plants were recorded. The presence and activities of ants associated with plants of *T. ulmifolia* were recorded at most populations. Ants were collected from populations 1, 2, 3, 7, 16 and preserved in alcohol for identification purposes.

Results

Floral Morphology

The varieties of *T. ulmifolia* utilized in this study differ from one another in a range of floral characters (Table 3, Fig. 1). The varieties *elegans*, *intermedia*, *surinamensis*, and *elegans* × *intermedia* are distylous. Populations of these taxa exhibit variation in the size of reproductive organs (Fig. 2), but the mean style and stamen lengths are distinct in the two floral forms and there is a reciprocal correspondence between the heights of stigmas and an-

thers (Table 4). The minimum distance separating reproductive organs tends to be smaller in long-styled flowers compared with short-styled flowers. This pattern is particularly evident in populations 6 (var. *intermedia*) and 22 (var. *surinamensis*).

Individuals of var. *angustifolia* grown from seed and in populations 5 and 7 are of a single floral form with long styles and mid- to long-level stamens. In this homostylous form, the minimum distance separating reproductive organs is similar to that recorded for the long-styled form of heterostylous varieties (Table 4).

In common with many distylous species, pollen dimorphism accompanies the differences in stamen and style lengths in the heterostylous varieties (Table 5). In each of the varieties, pollen grains from the long set of anthers are significantly larger than those from the short anther level, although some overlap in the size classes of pollen from different anther levels occurs. Pollen produced by populations of var. *angustifolia* is monomorphic for size.

Compatibility Relationships

A total of 88 plants of the distylous varieties was utilized in the controlled crossing program. Eighty-seven individuals were strongly self-incompatible, yielding little seed from self-pollinations (Table 6). A single plant, a long-styled form of var. *elegans* from Crato, Brazil, was highly self-compatible. A total of 14 self-pollinations conducted on this plant all resulted in seed production ($\bar{x}$ seed set per pollination 22.4, SD 9.8). In contrast to self-incompatible plants, the self-compatible individual was cross-compatible with other long-styled plants, when used as a pollen parent. Reciprocal own-form pollinations utilizing this individual as the egg parent resulted in no seed production.

Legitimate pollinations (between anthers and stigmas at equivalent levels) produced near maximal fruit production in each of the distylous varieties. In three of the four populations utilized there were significant differences between the seed production of floral forms. The mean seed set of short-styled forms of vars. *elegans* and *intermedia* was greater than that of long-styled forms in legitimate pollinations. In hybrid plants from Colombia, no significant difference in the seed production of floral forms was obtained from legitimate pollinations.

All individuals of var. *elegans* from Malaya were substantially less fecund than plants of the same variety from Brazil (Table 6). The mean seed set per pollination in Malaysian plants was 12.5 compared with 34.4 in plants from Brazil.

TABLE 1. Varietal status, locality, and habitat of populations of *Turnera ulmifolia* surveyed

Population	Variety	Locality	Habitat	Date studied
1	*intermedia*	Managua, Managua Dept., Nicaragua	Wasteground	July 1974
2	*intermedia*	Santa Rosa, Guanacaste Prov., Costa Rica	Roadside	November 1975
3	*intermedia*	La Pacifica, Guanacaste Prov., Costa Rica	Roadside	November 1975
4*	*intermedia*	Cañas, Guanacaste Prov., Costa Rica	Roadside	November 1975
5	*angustifolia*	Cañas, Guanacaste Prov., Costa Rica	Garden	November 1975
6†	*intermedia*	Chitre, Herrera Prov., Panama	Roadside	June 1977
7*†	*angustifolia*	Panama City, Panama Prov., Panama	Garden	July 1974
8	*intermedia*	Pacora, Panama Prov., Panama	Roadside	June 1977
9	*intermedia*	Chepo, Panama Prov., Panama	Roadside	June 1977
10	*intermedia*	El Sombrero, Guárico St., Venezuela	Roadside	July 1977
11	*intermedia*	Palo Seco, Guárico St., Venezuela	Wasteground	July 1977
12*†	*intermedia*	Calabozo, Guárico St., Venezuela	Roadside	July 1977
13	*elegans* × *intermedia*	Dagua, Valle Dept., Colombia	Roadside	August 1974
14	*elegans* × *intermedia*	Loboguerrero, Valle Dept., Colombia	Roadside	August 1974
15	*elegans* × *intermedia*	Loboguerrero, Valle Dept., Colombia	Wasteground	August 1974
16*†	*elegans*	Manaus, Amazonas St., Brazil	Wasteground	September 1974
17	*elegans*	Manaus, Amazonas St., Brazil	Wasteground	September 1974
18	*elegans*	Manaus, Amazonas St., Brazil	Roadside	July 1977
19	*elegans*	Itacoatiara, Amazonas St., Brazil	Wasteground	July 1977
20	*elegans*	Oriximina, Pará St., Brazil	Wasteground	July 1977
21	*elegans*	Santarém, Pará St., Brazil	Wasteground	July 1977
22*†	*surinamensis*	Santarém, Pará St., Brazil	Graveyard	July 1977
23*	*surinamensis*	Santarém, Pará St., Brazil	Wasteground	July 1977
24	*surinamensis*	Santarém, Pará St., Brazil	Wasteground	July 1977
25*	*surinamensis*	Almeirim, Pará St., Brazil	Roadside	November 1974
26	*elegans*	Boca de Jari, Amapa Terr., Brazil	Garden	September 1974
27*	*elegans*	Altamira, Pará St., Brazil	Wasteground	November 1974
28*	*elegans*	Belém, Pará St., Brazil	Graveyard	September 1974
29	*elegans*	Belém, Pará St., Brazil	Garden	September 1974
30*	*intermedia*	Barreirinhas, Maranhão St., Brazil	Wasteground	August 1977

NOTE: All populations were sampled for style form representation (see Table 7). *, populations sampled for seed fecundity (see Table 10); †, populations sampled for floral and pollen measurements (see Tables 4, 5).

TABLE 2. Source and varietal status of plants of *Turnera ulmifolia* utilized in controlled pollination studies

Collection No.	Variety	Locality	No. plants utilized
Barrett RU72-222 UR	*elegans*	Crato, Brazil	35
Stone and Ojima 12111 KLU	*elegans*	Selangor, Malaya	14
Barrett 1125 UC	*intermedia*	Caracas, Venezuela	16
Barrett 689 UC (population 13)	*elegans* × *intermedia*	Dagua, Colombia	23
Barrett 670 UC (population 7)	*angustifolia*	Panama City, Panama	7
Stone 12149 KLU	*angustifolia*	Selangor, Malaya	5

Plants of homostylous var. *angustifolia* from Malaya and Panama are self-compatible and moderately autogamous. Self-pollination occurs at the completion of flowering. The reflexed anthers are brought into contact with the stigmas by the withering of perianth parts. Twenty-one capsules resulting from autogamy in var. *angustifolia* yielded a mean of 49.5 seeds per capsule.

Population Structure

Populations of distylous varieties of *T. ulmifolia* are usually composed of long- and short-styled plants. In 27 of the 28 populations surveyed, both floral forms were represented (Table 7). Statistically significant isoplethy occurred in 24 populations.

Short-styled plants of var. *elegans* at Boca de

TABLE 3. Characters distinguishing varieties of *Turnera ulmifolia*

Character	*angustifolia*	*elegans*	*intermedia*	*surinamensis*
Life-form	Perennial, sub shrub to 1–2 m	Herbaceous to woody perennial to 1.5 m	Herbaceous to woody perennial to 1 m	Herbaceous to woody perennial to 0.75 m
Chromosome no.*	$n = 15$	$n = 10$	$n = 5, 10, 15?$	?
Breeding system	Homostylous, self-compatible	Heterostylous, self-incompatible	Heterostylous, self-incompatible	Heterostylous, self-incompatible
Mean flower diameter, mm	54.1	50.8	39.9	30.6
Mean petal length × breadth, mm	34.5 × 21.7	32.6 × 23.0	24.1 × 17.2	21.4 × 11.7
Flower colour	Deep yellow	Cream with dark spot	Pale to deep yellow	Pale blue
Distribution	West Indies, introduced to Central America? and Old World	Brazil, introduced to Old World	Central and South America, Caribbean	Guianas, Brazil, Mexico

NOTE: Quantitative data for floral characters ($n = 10$) from populations 7, 16, 6, 22.
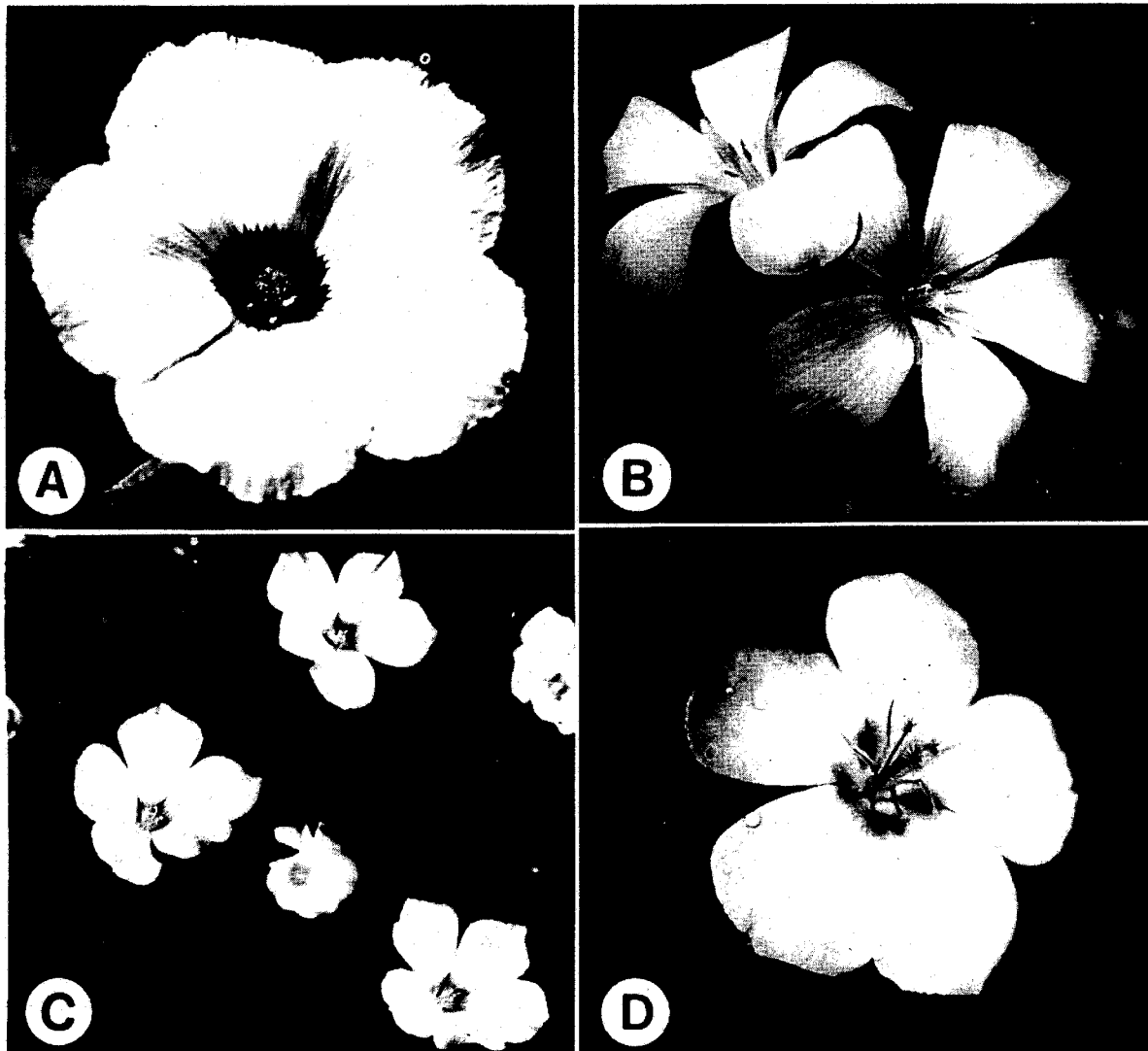*, from published counts and Barrett (unpublished).

FIG. 1. Varieties of *Turnera ulmifolia*: (A) var. *elegans* (long styled); (B) var. *intermedia* (short styled); (C) var. *surinamensis* (short styled); (D) var. *angustifolia* (homostyled).
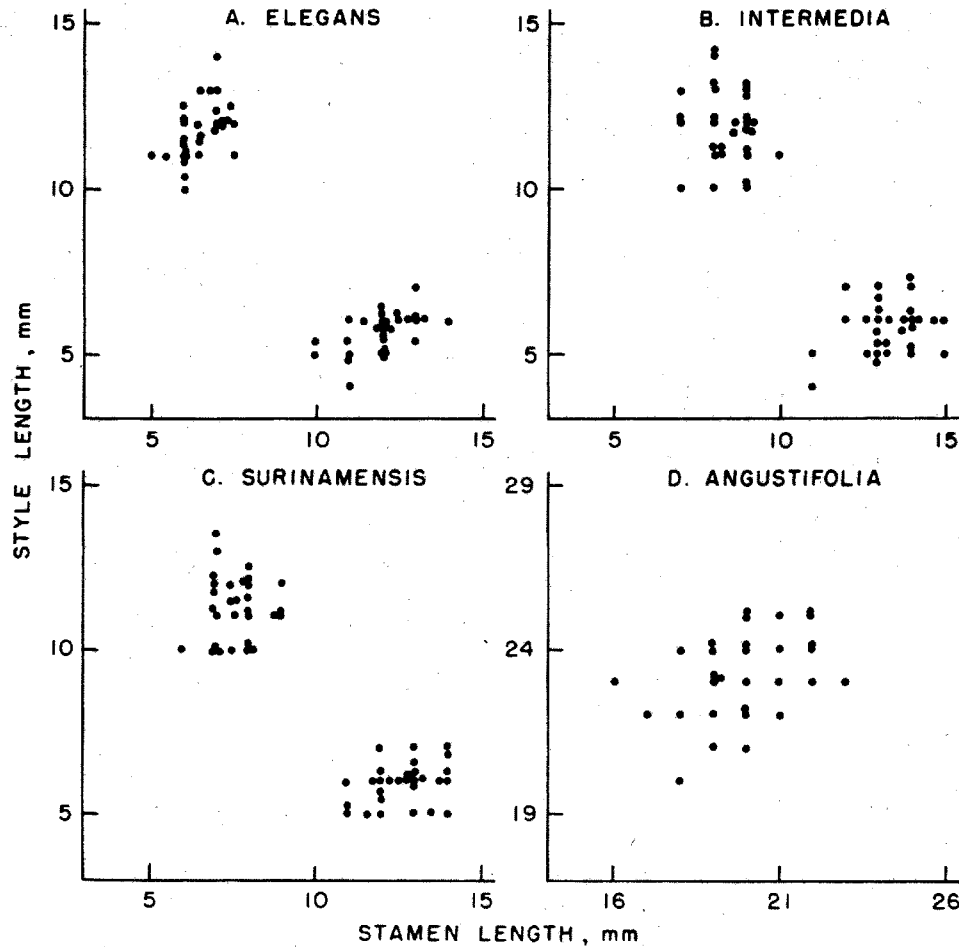
FIG. 2. Stamen and style lengths of individual plants in natural populations of *Turnera ulmifolia*: (A) population 16, var. *elegans*; (B) population 6, var. *intermedia*; (C) population 22, var. *surinamensis*; (D) population 7, var. *angustifolia*.

TABLE 4. Length of reproductive organs (mean and standard deviation in millimetres) in populations of *Turnera ulmifolia*

	Long-styled form			Short-styled form		
Population	Mean style length	Mean stamen length	Mean stigma–anther separation	Mean style length	Mean stamen length	Mean stigma–anther separation
6 *intermedia*	11.8±1.1	8.4±0.8	1.3±1.0	5.8±0.8	13.3±1.0	4.2±0.9
7 *angustifolia* (homostyle)	23.2±1.3	19.9±1.6	1.5±1.4			
12 *intermedia*	10.7±0.9	5.9±0.5	1.7±0.6	5.8±0.4	11.5±0.5	2.4±0.6
16 *elegans*	11.8±0.9	6.5±0.6	2.4±0.9	5.7±0.7	12.0±0.9	2.9±0.6
22 *surinamensis*	11.3±1.0	7.7±0.8	1.7±0.7	5.9±0.7	12.7±0.9	3.7±0.9

Jari, Amazônia (population 26) were introduced to the settlement in the early 1960s for ornamental purposes. Propagation from stem cuttings and root-borne shoots accounts for the monomorphic structure of this population.

Populations of *T. ulmifolia* are usually composed of colonies of closely grouped plants (Fig. 3A) and isolated individuals are relatively uncommon.

Flowering Phenology

In varieties *elegans*, *angustifolia*, *intermedia*, and *elegans* × *intermedia*, flowering commences 9–14 weeks after seed germination under glasshouse conditions. In young plants reproductive shoots produce flowers on alternate days, but flower production is almost continuous in vigorous, mature individuals. Under field conditions, large

TABLE 5. Measurements of the diameter (mean and standard deviation in micrometres) of pollen grains in populations of *Turnera ulmifolia*

Population	Long-styled form	Short-styled form	t^*
6 *intermedia*	65.75±3.90	76.50±3.12	21.48
7 *angustifolia*	83.62±3.15	Homostyle	—
16 *elegans*	70.43±4.31	82.52±3.92	20.84
22 *surinamensis*	64.88±3.03	75.69±3.45	23.43

*All comparisons of means significant at $P < 0.001$.

TABLE 6. Controlled pollinations of distylous varieties of *Turnera ulmifolia*

Cross,* ♀ × ♂	Plants tested	No. flowers pollinated	No. capsules produced	Percentage fruit set	No. seeds produced	Mean seed set per pollination	Standard deviation
			Variety *elegans* (Crato, Brazil)				
L × S	18	237	237	100	7212	30.4₊	13.0
S × L	17	172	172	100	6845	39.8†	13.8
L self	18	77	4	5.2	81	1.1	4.7
S self	17	55	1	1.8	7	0.1	0.9
L × L	18	62	3	4.8	49	0.8	3.5
S × S	17	24	0	0	0	0	0
			Variety *elegans* (Selangor, Malaya)				
L × S	7	111	100	100	1107	10.0₊	4.4
S × L	7	95	95	100	1477	15.6†	7.5
L self	7	40	0	0	0	0	0
S self	7	23	0	0	0	0	0
L × L	7	21	1	4.8	3	0.1	0.7
S × S	7	16	0	0	0	0	0
			Variety *intermedia* (Caracas, Venezuela)				
L × S	8	73	73	100	1077	14.8₈	6.8
S × L	8	75	75	100	1989	26.5§	8.3
L self	8	35	0	0	0	0	0
S self	8	66	2	3.0	7	0.1	0.9
L × L	8	9	0	0	0	0	0
S × S	8	13	0	0	0	0	0
			Variety *elegans* × *intermedia* (Dagua, Colombia)				
L × S	10	82	82	100	1632	19.9‖	7.2
S × L	13	70	70	100	1274	18.2‖	7.4
L self	10	31	1	3.2	3	0.1	0.5
S self	13	56	4	7.1	11	0.2	0.8
L × L	10	22	6	27.3	90	4.1	7.9
S × S	13	25	1	4.0	5	0.2	1.0

*L, long-styled form; S, short-styled form.
†$P < 0.001$; $t = 6.97$.
‡$P < 0.001$; $t = 6.40$.
§$P < 0.001$; $t = 9.39$.
‖Not significant; $t = 1.43$.

plants of vars. *elegans* and *angustifolia* produce between 50 and 150 flowers on a single day. Due to the smaller stature of vars. *intermedia*, *surinamensis*, and *elegans* × *intermedia*, daily flower production is considerably lower than in the other two varieties.

The flowering phenology of *T. ulmifolia* varies in different parts of its range. In humid forest zones such as Amazônia, where sufficient moisture is available, plants flower throughout the year (see Ball 1933; Martin 1965). In strongly seasonal climates, with savanna or caatinga vegetation, flower-ing is more pronounced during the wet season. Depending on the severity of the dry season, *T. ulmifolia* acts as an annual, dying back altogether during drought periods, e.g. NE Brazil (S. Barrett, personal observation), Llanos, Venezuela (M. Kalin Arroyo, personal communication).

Individual flowers of *T. ulmifolia* open between 7:00 and 8:00 a.m. and close 3–4 h later. Dull or cool weather delays flowering by several hours. A single flower opens for 1 day only. There were no differences among the heterostylous varieties in the anthesis period of individual flowers under glasshouse

TABLE 7. Representation of floral forms in New World populations of
Turnera ulmifolia

Population	Long style	Short style	Homostyle	Total	χ^2
1	9	3	—	12	—*
2	25	20	—	45	0.56
3	47	49	—	96	0.04
4	107	103	—	210	0.08
5	—	—	9	9	—
6	94	100	—	194	0.19
7	—	—	35	35	—
8	63	71	—	134	0.48
9	78	65	—	143	1.18
10	39	40	—	79	0.01
11	107	112	—	219	0.11
12	122	119	—	241	0.04
13	51	54	—	105	0.09
14	84	72	—	156	0.92
15	49	57	—	106	0.60
16	267	236	—	503	1.91
17	155	153	—	308	0.01
18	133	137	—	270	0.06
19	34	36	—	70	0.06
20	28	35	—	63	0.78
21	53	80	—	133	5.48*
22	74	76	—	150	0.03
23	127	129	—	256	0.02
24	11	9	—	20	0.20
25	1	1	—	2	—
26	0	55	—	55	—*
27	167	179	—	346	0.42
28	527	558	—	1085	0.89
29	1	3	—	4	—*
30	62	64	—	126	0.03

*Significant deviation from 1:1.

conditions. However, flowers of homostylous var. *angustifolia* remain open for 2–3 h longer than flowers of heterostylous plants.

Pollination

The prolific flowering and showy entomophilous flowers of *T. ulmifolia* attract a wide range of insect visitors which feed on pollen and nectar (Table 8). *Turnera ulmifolia* is probably an important food source for many insects since it occurs in plant communities composed of weed species with relatively inconspicuous flowers and limited food rewards. The most frequent visitors to flowers of *T. ulmifolia* were skippers (Hesperiidae, Fig. 3B), small pollen-collecting bees (*Trigona* and Halictidae), and the introduced honey bee (*Apis mellifera* L.). These species probably vary in their effectiveness as pollinators of *T. ulmifolia*.

Observations of the foraging activity of skippers at population 28 (var. *elegans*) suggest that these particular lepidopterans do not show any preference for either style form as a food source (Table 9). Of a total of 223 flights to plants recorded over a 3-h period, 111 were to long-styled forms and 112 were

to short-styled individuals. Although var. *elegans* produces a large number of flowers on an individual plant (Fig. 3A), the majority of skipper visits (78.0%) were to one or two flowers per plant. A similar pattern of foraging was observed in anthophorid bees (*Exomalopsis* sp.) in population 16 at Manaus. Seventy-three percent of the visits to plants were to either one or two flowers per plant. It is not clear why these different groups of insects do not visit more flowers on an individual before departing, but the foraging pattern must reduce the likelihood of pollinations between flowers on the same plant (geitonogamy).

Seed Fecundity

Seed production occurred in all populations with the exception of population 26 at Boca de Jari. There were no significant differences in seed set per capsule between the two floral forms in each of the nine heterostylous populations sampled for seed fecundity (Table 10).

Population 30 (var. *intermedia*) at Barreirinhas, Brazil, is polymorphic for a dark brown spot at the base of the corolla. The spotted morph represents

TABLE 8. Insect visitors to flowers of *Turnera ulmifolia*

| Insect visitor	Population	Food source utilized
Diptera		
Bombyliidae	16	Pollen and nectar
Syrphidae	29	Pollen
Hymenoptera		
Apis mellifera L. (Apidae)	7, 19, 22, 27, 29	Pollen and nectar
Eulaema nigrita Lep. (Apidae)	29	Pollen and nectar
Eulaema sp. 2 (Apidae)	29	Pollen and nectar
Trigona spp. (Meliponidae)	16, 22	Pollen and extra floral nectar
Exomalopsis sp. (Anthophoridae)	16	Pollen and nectar
Epicharis sp. (Anthophoridae)	29	Pollen and nectar
Centris sp. (Anthophoridae)	16	Pollen and nectar
Polistes (Vespidae)	29	Extra floral nectar
Halictidae	3, 5, 7, 22, 29	Pollen
Lepidoptera		
Hesperiidae	1, 3, 5, 6, 12, 16, 22, 27, 29	Nectar
Large Lepidoptera	3, 22, 29	Nectar
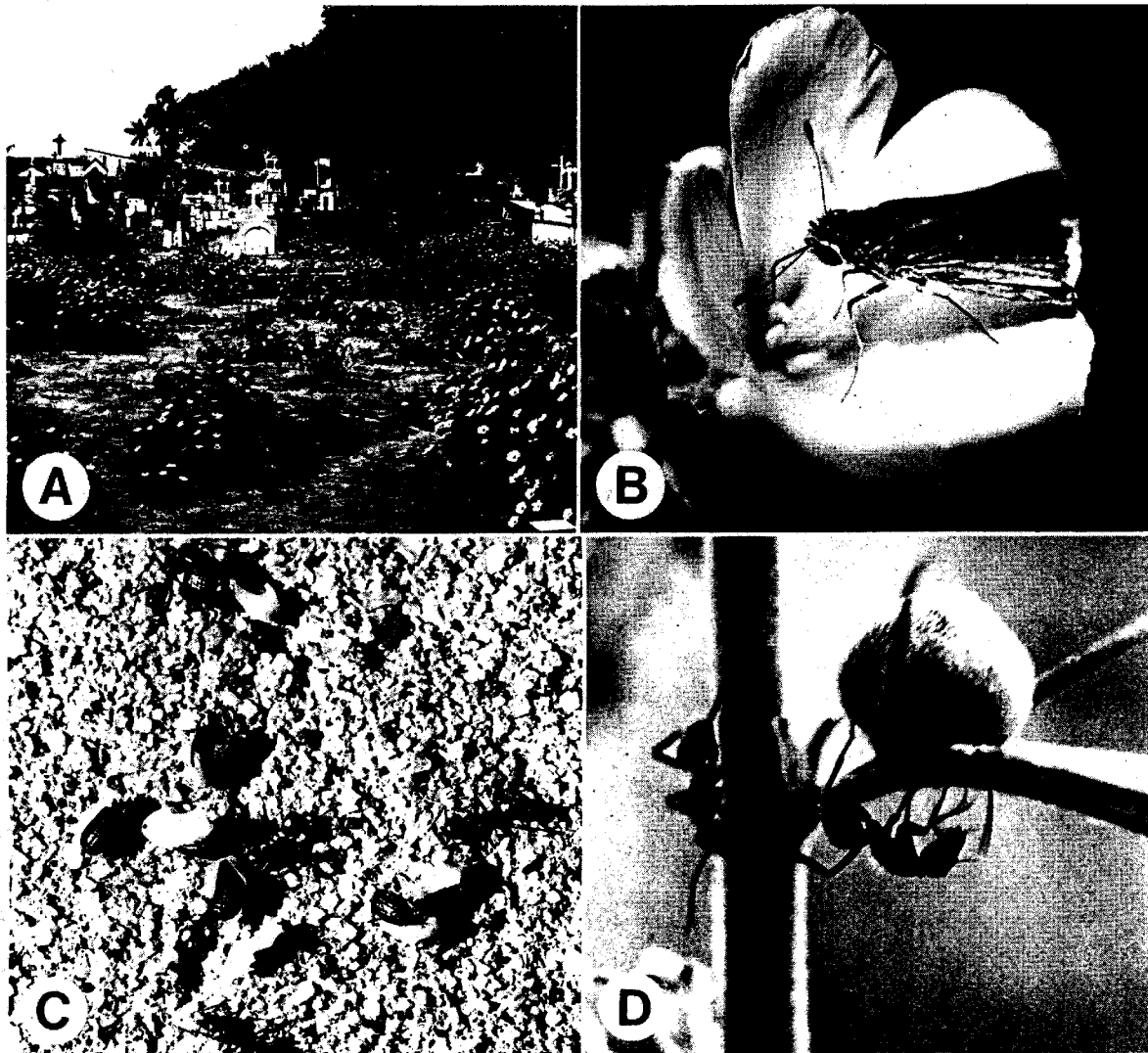
FIG. 3. (A) Population 28 of *Turnera ulmifolia* var. *elegans*, Belém, Brazil. (B) Skipper feeding on nectar from flower of *T. ulmifolia* var. *intermedia* (population 1). (C) Ants transporting seeds of *T. ulmifolia* var. *angustifolia* (population 7). Note the white, fleshy aril attached to seeds. (D) Ant (*Ectatomma* sp.) feeding from extrafloral nectaries of *T. ulmifolia* var. elegans (population 16). Note the position of nectaries below the seed capsule.

TABLE 9. Foraging patterns of insect visitors to flowers of *Turnera ulmifolia*

| No. flowers visited per plant visit | No. plants | | Total plants | Percentage of total visits |
	Long-styled	Short-styled		
Solitary bee (Hymenoptera, *Exomalopsis*), population 16 (var. *elegans*, Manaus)				
1	23	35	58	49.6
2	12	16	28	23.9
3	6	3	9	7.7
4	5	9	14	12.0
5	0	4	4	3.4
>5	1	3	4	3.4
Total	47	70	117	100
Skipper (Lepidoptera, Hesperiidae), population 28 (var. *elegans*, Belém)				
1	61	58	119	53.3
2	32	23	55	24.7
3	9	20	29	13.0
4	4	8	12	5.4
5	2	1	3	1.3
>5	3	2	5	2.3
Total	111	112	223	100

TABLE 10. Seed fecundity of floral forms in New World populations of *Turnera ulmifolia*

| Population | Long-styled form | | | Short-styled form | | |
	No. capsules sampled	Mean seeds per capsule	Standard deviation	No. capsules sampled	Mean seeds per capsule	Standard deviation
4 *intermedia*	100	13.6	9.0	120	12.4	9.7
12 *intermedia*	65	10.0	7.7	67	10.1	9.6
16 *elegans*	202	16.6	7.3	221	17.1	6.6
22 *surinamensis*	30	21.0	8.8	30	24.3	13.1
23 *surinamensis*	89	19.1	8.2	106	18.3	8.5
25 *surinamensis*	16	12.4	4.3	12	11.3	8.5
27 *elegans*	114	14.7	7.2	120	16.7	12.0
28 *elegans*	127	16.4	8.7	129	14.9	8.3
30 *intermedia*	111	20.2	10.9	110	19.5	12.7

NOTE: All comparisons of means are not significant at $P = 0.001$.

7.0% of the plants in the population and includes both long- and short-styled forms. There were no significant differences in seed set per capsule between the spotted ($\bar{x} = 18.8$, SD $= 12.1$, $n = 152$) and unspotted ($\bar{x} = 19.8$, SD $= 11.8$, $n = 221$) morphs within the population.

Twenty capsules harvested from the small garden population of homostylous var. *angustifolia* in Panama (population 7) averaged 74.3 seeds per capsule (SD $= 22.8$).

Seed Dispersal

Seeds of *T. ulmifolia* are scattered to the ground during capsule dehiscence, which occurs from 20 to 30 days after fertilization. Attached to the narrow end of the 2- to 3-mm-long seed is a shield-shaped aril (Fig. 3C). The aril is soft, white, and contains fat bodies (elaiosomes) and starch, which are attractive to ants as a food source (Lock 1904; Van der Pijl 1972). Lock (1904) reported seed dispersal by ants (myrmecochory) in introduced populations of var. *elegans* on Sri Lanka. At populations 3 (var. *intermedia*), 7 (var. *angustifolia*), and 16 (var. *elegans*), ants were observed both feeding on the arils of *Turnera* seeds and transporting seeds into ant holes in the vicinity of *T. ulmifolia* plants (Fig. 3C). At each population, seeds freshly harvested from capsules were scattered around ant holes. Within 1 h almost all seeds had been transported into holes by ants. The observed maximum distance for seed dispersal by an ant was 3 m.

Turnera ulmifolia possesses both floral and extrafloral nectaries (Elias *et al.* 1975). Paired extrafloral nectaries occur on the petiole near the

TABLE 11. Ants associated with *Turnera ulmifolia*

Population	Ant species	Activity
1. Managua, Nicaragua (var. *intermedia*)	*Ectatomma ruidum* Roger, and *Solenopsis geminata* (Fabricius)	Feeding at extrafloral nectaries
2. Santa Rosa, Costa Rica (var. *intermedia*)	*Ectatomma ruidum* Roger, *Pseudomyrmex gracilis* (F. Smith), *Monomorium ebininum* Forel, and *Camponotus rectangularis* Emery	Feeding at extrafloral nectaries
3. La Pacifica, Costa Rica (var. *intermedia*)	*Crematogaster brevispinosa* Mayr, and *Paratrechina longicornis* (Latreille)	Feeding at extrafloral nectaries and transporting seeds
7. Panama City, Panama (var. *angustifolia*)	*Ectatomma ruidum* Roger, *Acromyrmex octospinosus* (Reich), and *Azteca alfari* Emery	Feeding at extrafloral nectaries and transporting seeds
16. Manaus, Brazil (var. *elegans*)	*Ectatomma ruidum* Roger, *Ectatomma quadridens* (Fabricius), *Camponotus naegelii* Forel?, *Odontomachus bauri* Emery, *Solenopsis globularia* F. Smith, *Acromyrmex hystrix* (Latreille), *Pheidole* sp. 1, and *Pheidole* sp. 2	Feeding at extrafloral nectaries and transporting seeds

developing seed capsule (Fig. 3D). Ants were observed feeding from foliar nectaries at the majority of populations investigated in this study. A total of 16 species of ants was collected from *T. ulmifolia* plants (Table 11). *Ectatomma ruidum* Roger was found associated with *T. ulmifolia* plants in Nicaragua, Costa Rica, Panama, and Brazil. At populations 3, 7, and 16 the same species of ants were observed both transporting seeds and feeding on extrafloral nectar (Table 11).

Discussion

Heterostylous breeding systems are reported from 24 flowering plant families representing diverse phyletic assemblages (Vuilleumier 1967). In some families, such as the Turneraceae and Rubiaceae, a large proportion of taxa is heterostylous (Urban 1883; Bir Bahadur 1968); whereas in other families, e.g. Leguminosae and Saxifragaceae (Vogel 1955; Ornduff 1971), few species exhibit this type of floral polymorphism. Despite the incongruence in taxonomic affinity among heterostylous families, the syndrome of characters associated with floral heteromorphism is similar and usually includes a reciprocal arrangement of style and stamen lengths, self-incompatibility, and pollen heteromorphism (Vuilleumier 1967).

The expression of heterostyly in the *T. ulmifolia* complex is typical of many heterostylous families. The results of controlled pollinations confirm earlier studies by Lock (1904) and Martin (1965), both of whom demonstrated the association of a self-incompatibility system with floral dimorphism. Martin (1965) documented wide variation in the

size of reproductive organs in the two floral forms of *T. ulmifolia* in Puerto Rico. He interpreted this pattern of variation as an indication that "the morphological features of distyly in *T. ulmifolia* are not well co-ordinated" and that heterostyly in *T. ulmifolia* is "less developed or incomplete" compared with other heterostylous species. There are difficulties in accepting this interpretation. Although variation in the size of floral organs of *T. ulmifolia* was also obtained in the present study, a review of distyly (Ganders 1975) provides evidence which suggests that this may be a general feature of most distylous plants.

Lock (1904) found that the seed production of the long-styled form of var. *elegans* in Sri Lanka was considerably greater than that of the short-styled form under conditions of open pollination. In the present study, it was not possible to detect differences in the seed fecundity of floral forms in the nine heterostylous populations sampled. However, in artificial pollinations of Brazilian and Malaysian plants of var. *elegans* under glasshouse conditions, average seed set was greater in the short- than the long-styled form.

Substantial differences in seed fecundity were evident between Brazilian and Malaysian plants of var. *elegans*, with Brazilian genotypes producing two to three times more seeds than Malaysian plants following legitimate pollinations. The levels of seed production obtained from controlled pollinations and in natural populations of Brazilian plants were also considerably higher than values reported from Sri Lanka (Lock 1904) and Indonesia (Van Steenis 1931). This suggests that populations

in parts of the adventive range of var. *elegans* may be less fertile than those from Brazil. Evidence to support this suggestion comes from cytological studies. Raman and Kesavan (1964) report abnormalities including univalents and laggards in 63% of meiotic cells observed in var. *elegans* from India. Similar meiotic aberrations were observed in Malaysian plants utilized in this study (S. Barrett, unpublished data) and pollen stainability was low ($\bar{x}$ pollen stainability 59.7%, $n = 30$ flowers, range 31–78%). In contrast, pollen stainability in Brazilian plants was in excess of 95% and meiosis appeared normal. The reduced fertility of some Asian plants could be the result of the chance introduction to Asia of infertile genotypes or subsequent reduction in fertility due to 'inbreeding' within a limited, introduced gene pool. In a self-incompatible species this is likely to expose deleterious genes, normally sheltered in the heterozygous condition, and lead to inbreeding depression (Stebbins 1957).

Although heteromorphic incompatibility is strongly developed in the *T. ulmifolia* complex, occasional individuals are self-compatible. A single plant of var. *elegans* among a total of 49 individuals tested was found to be thoroughly self-compatible. Pollen of the exceptional plant was capable of producing seed in own-form pollinations, but in reciprocal own-form pollinations no seed was obtained. These findings indicate modifications in the incompatibility behavior of pollen grains, rather than stylar tissue. Such modifications are independent of pollen size since the self-compatible individual produced pollen of a similar size to other long-styled plants. Breakdown of self-incompatibility can result from loss of S-allele activity, S-locus duplication, or a change in the action of major or minor genes upon the S locus. The appearance of rare self-compatible individuals appears to have little influence on the population structure and overall functioning of outbreeding in heterostylous varieties of *T. ulmifolia*.

It has been suggested that the most efficient breeding structure in populations of heterostylous plants is one in which the floral forms are equally represented (Mather and De Winton 1941). Although *T. ulmifolia* populations occur in disturbed habitats and are often recently established, the predominant population structure is one of isoplethy. No formal genetic analysis of style form was undertaken in this study, but families obtained from open-pollinated plants segregated equal numbers of style forms. This finding, taken in conjunction with the data on population structure, suggests that the inheritance of style form in *T. ulmifolia* may be of the conventional '*Primula* type' with a single locus

and two alleles (Ss, ss), one of which is a simple Mendelian dominant (Bateson and Gregory 1905). With this inheritance pattern and complete disassortative mating guaranteed through strong self-incompatibility, a 1:1 morph ratio could be obtained in one generation regardless of the initial frequency of forms in founder populations (Haldane 1936).

In common with other heterostylous groups, the *T. ulmifolia* complex contains heterostylous and homostylous forms. Darwin (1877) introduced the term homostyly to refer to plants which are evolutionarily derived from heterostylous ancestors and possess anthers and stigmas at equivalent levels within a flower. Small-flowered, self-compatible, homostylous forms have since been described from several heterostylous families (Baker 1959, 1961; Ornduff 1972, 1976).

Turnera ulmifolia var. *angustifolia* differs in several respects from typical homostylous forms. The flowers are larger in size than those of heterostylous forms in the complex. This indicates that there are exceptions to the commonly held view, that flower size in self-compatible species is smaller than in closely related self-incompatible species (Lewis 1956; Lloyd 1965; Bawa and Opler 1975). In homostylous flowers of var. *angustifolia* anthers are positioned below the stigmas of long styles. Hence during flowering the anthers and stigmas are not in contact and self-pollination occurs after anthesis. Insects visit flowers of var. *angustifolia* for pollen and nectar, and it is likely that under field conditions considerable outcrossing occurs. The seed fecundity of naturally pollinated plants from Panama was 33.4% higher than values obtained from autogamous seed set under glasshouse conditions. Whether or not var. *angustifolia* is strictly homostylous in the Darwinian sense is not clear. Detailed biosystematic studies are necessary to confirm whether var. *angustifolia* is a derivative of a heterostylous ancestor.

In several heterostylous families, such as the Oxalidaceae, Boraginaceae, and Sterculiaceae, the evolution of homostyly and self-compatibility is associated with increased colonizing ability and the development of the weedy habit (Baker 1959; Ornduff 1971, 1976; Martin 1967). In the *Turnera ulmifolia* complex, homostylous forms show no greater propensity to become weeds than do the heterostylous varieties. Indeed, throughout Central America and Venezuela, heterostylous var. *intermedia* is the most commonly encountered weed form in the complex. In northern Brazil, var. *intermedia* is replaced by heterostylous var. *elegans* as the predominant weed of waste ground. Adven-

tive populations of var. *elegans* and homostylous var. *angustifolia* have achieved similar ranges in the Old World.

In temperate regions there are few heterostylous weeds. Temperate weeds are usually characterized by inconspicuous flowers, self-compatibility, and autogamous breeding systems (Baker 1955, 1965, 1974; Mulligan and Findlay 1970). However, in the tropics a number of heterostylous species are reported as weeds. These include *Melochia* and *Waltheria* spp. (Martin 1967; Cardenas *et al.* 1972), *Eichhornia crassipes* (Barrett 1977a), *Pontederia* spp. (Bristow *et al.* 1972; Barrett 1977b), *Nymphoides humboldtiana* (= *indica*) (Dirven and Poerink 1955; Bristow *et al.* 1972), and *Oxalis* spp. (Baker 1965).

The difference in the number of heterostylous weeds between the two areas probably reflects the greater number of perennial weeds in tropical regions. Outbreeding mechanisms, such as heterostyly, appear to have developed more commonly in association with the perennial, rather than the annual, life-form. Nevertheless, heterostyly associated with diallelic incompatibility poses certain restrictions on colonizing ability, since population establishment requires the chance introduction of both incompatibility groups to a site. Where weediness has developed in heterostylous groups it is frequently associated with vigorous clonal propagation and (or) the breakdown of self-incompatibility (Martin 1967; Barrett 1977a, 1977b). However, in *T. ulmifolia* self-incompatibility is strongly developed in the heterostylous varieties, and vegetative reproduction is of relatively limited importance. It is, therefore, of interest to examine those features which have enabled *T. ulmifolia* to become a widespread tropical weed, in spite of a breeding system which might be expected to restrict colonizing ability.

The perennial habit of *T. ulmifolia* plants and their capacity for continuous flower production enhance opportunities for successful matings. In addition, these traits give the species considerable reproductive potential. Daily seed output in excess of 200 seeds is not unusual for mature individuals of vars. *angustifolia* and *elegans*. Ball (1933) has shown that 60% of the dry matter present in corollas of var. *elegans* is translocated back into the shoot before flowers are shed and thus assimilates are available for the production of subsequent flowers. This pattern of resource allocation presumably aids in maintaining continuous flower production.

Although *T. ulmifolia* has a high reproductive capacity, there is some evidence that, unlike many successful weeds, the species appears to lack great powers of natural seed dispersal over long distances. Seeds of *T. ulmifolia* are not particularly small for a weed species and they do not possess adaptations for long distance dispersal. Dispersal of *T. ulmifolia* is primarily by ants, which have only limited powers of dispersal in terms of distance (Van der Pijl 1972).

Field observations of natural populations support the view of limited distance dispersal in *T. ulmifolia*. The majority of New World populations observed in this study were composed of colonies of closely grouped individuals and isolated plants were rather uncommon. In Amazônia, naturalized populations of var. *elegans* flourish on waste ground in the vicinity of settlements, but as yet there has been little invasion of the disturbed habitats along the edges of roads linking the towns. Other widespread tropical weeds with greater dispersal powers have rapidly colonized roadside habitats.

Detailed studies of ant dispersal in *T. ulmifolia* are required in order to document the mechanism and rate of invasion of disturbed habitats. At this stage it would appear that the dispersal system of *T. ulmifolia* is suitably coadapted with the population requirements of the breeding system. The social behavior of ants associated with *T. ulmifolia* tends to concentrate seeds in localized areas. This pattern of seed dispersal favors the establishment of dense colonies of plants and increases the likelihood of seed set.

In contrast to the limited powers of natural dispersal in *T. ulmifolia*, human factors have probably played a more important role in enlarging the overall range of the species and providing an opportunity for the exploitation of new disturbed habitats. The large, showy flowers and profuse flowering habit of vars. *angustifolia*, *elegans*, and *intermedia* give these forms considerable horticultural value and their ranges have been greatly expanded as a result of their use as garden plants (Lock 1904; Backer 1951; Brizicky 1961; Martin 1965). The future increase in disturbed habitats associated with human settlement in tropical regions is likely to favor further spread of the *T. ulmifolia* complex.

Acknowledgments

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