

Reproductive success in the tropical weed *Triumfetta semitriloba* (Tiliaceae): spatial and temporal variation in seed set

Rosane G. Collevatti^{1,4}, Frederico S. Lopes² and Maria Eugênia C. Amaral³

- ¹ Setor de Ecologia, Departamento de Biologia Geral, Universidade Federal de Viçosa, Viçosa, MG, Brasil. 36570-000.
² Departamento de Ciências Naturais, Universidade do Rio de Janeiro, Rio de Janeiro, RJ, Brasil. **Present address:** Setor de Ecologia, Departamento de Biologia, Universidade Federal do Mato Grosso do Sul, Campo Grande, MS. Brasil.
³ Setor de Ecologia, Departamento de Biologia, Universidade Federal do Mato Grosso do Sul, Campo Grande, MS. Brasil.
⁴ **Correspondence to:** Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, C.P. 04631, Universidade de Brasília, Brasília, DF. Brazil. 70919-970. email: rosanegc@guarany.cpd.unb.br

Received 15-II-1997. Corrected 20-VIII-1997. Accepted 18-IX-1997.

Abstract: Reproduction of *Triumfetta semitriloba* Jacq. (Tiliaceae), a facultatively autogamous tropical shrub weed, was studied in three patches of different habitat "quality", in Viçosa, Southeastern Brazil. In each patch ten plants were randomly chosen to collect 25 fruits per plant, during each flowering month (March, April and May) in 1994. Mean seed initiation and seed set, pooling all patches and flowering months were 2.535 (sd=0.145) and 1.487 (sd=0.102), respectively (maximum: six seeds per fruit). Mean seed abortion was 41.3%. There was a higher number of initiated seeds per fruit in one patch, probably caused by differences in patch "quality" and pollinator abundance, and not by spatial differences on seed abortion, which was not different among patches. Two patches had the same temporal variation (among flowering months) in seed set. The greater brood size during the first and last months was caused by a higher seed initiation on the first flowering month and higher proportion of seed abortion on the second month. On the second month there were more flowers per plant, which may lead to a lower rate of cross-pollination and, consequently, lower seed set. The differing patch had a greater brood size during the first and second months. This pattern could be a result of a higher seed initiation on the first flowering month, or of other patch characteristics such as lower number of flowers per plant, or lower abundance of pollinators, especially during the last month, and a high rate of flower predation by beetle species, but not by differences in seed abortion among months.

Key words: Reproductive success, seed set, seed abortion, *Triumfetta semitriloba*, Tiliaceae, weed.

The reduction in brood size (reduction in the number of initiated seeds that mature within a single fruit) and consequently in reproductive success, is common in hermaphrodite species and could play an important effect on plant fitness and evolution of reproductive traits (Shaanker et al. 1988, Marshall and Folsom 1991, O'Donnell and Bawa 1993). This reduction may be the outcome of genetic load manifestation, resource depletion, pre-dispersal seed predation, maternal regulation of offspring quality (infanticide), and sibling rivalry (fratricide) (Lee 1988, Shaanker et al. 1988, Marshall and Folsom 1991).

Plant species may have a spatial and tem-

poral variability in reproductive success. Differences between populations in pollinators abundance, nutrient and water availability, and herbivory may produce heterogeneity in brood reduction, leading to a spatial pattern in seed set (Bertin 1988, Hendrix 1988, Ågren 1989, Coffin and Lauenroth 1992). Likewise, heterogeneity in brood reduction along the flowering season, especially in species with a long flowering season, may lead to a temporal variation in individual reproductive success (Zimmerman and Gross 1984, Jennersten et al. 1988, English-Loeb and Karben 1992, Stephenson 1982, Haig and Westoby 1988).

This work aimed to study the spatial and

TABLE 1

Characteristics of the three studied patches of *T. semitriloba* in Viçosa, Southeastern Brazil.

Patch	Size (m ²)	Mean number of flowers per patch ¹	Standard deviation	Shape and locality characteristics
P1	200	21.505	13.659	Square/abandoned pasture on a hill
P2	100	48.180	44.412	Square/abandoned pasture on a plane river-side
P3	200	2.250	4.879	Very narrow rectangle composed of two parallel lines of individual plants/forest trail

¹ Mean number of flowers per patch was calculated as mean number of opened flower per plant, pooling all days (in Collevatti 1995).

temporal pattern of *Triumfetta semitriloba* Jacq. (Tiliaceae) reproductive success, focusing on among patches and among flowering months variation on seed initiation, seed set and abortion

MATERIALS AND METHODS

Study species and site: *T. semitriloba* is a facultatively autogamous shrub weed species, occurring in well delimited patches in abandoned pastures, secondary forests gaps and road sides in tropical America. In Southeastern Brazil, flowering occurs in autumn (March to May) and buds open in the afternoon. Despite the existence of five floral nectaries around the ovary base, nectar production is negligible. Flower visitors are mainly solitary bee species, although social bee species, beetles, flies, bugs and butterflies have also been recorded

(Collevatti *et al.* in prep.).

Three patches, of different habitat "quality" was chosen for field work (Table 1), in Viçosa, Southeastern Brazil (20°45'S, 42°50'W). All individuals in each patch were marked and numbered and field work was conducted in the flowering season of 1994 (March to May).

Methods and statistical analysis: Ten plants were randomly chosen, in each patch, and 25 fruits were collected from each plant, in each flowering month. Fruits have three locules with two ovules each, resulting in a maximum of six seeds per fruit. Ripened fruits were opened and number of follicles that initiated development (initiated seeds) and the number of mature seeds per fruit (seed set) were counted. A tetrazolium test of viability was used to confirm seed viability and abortion. Seed abortion was defined as the proportion [1-(seed set/initiated seeds)].

TABLE 2

Mean number of initiated seeds and seed set per fruit, standard deviation and proportion of seed abortion, for *T. semitriloba*, in each patch, pooling all months.

Patch	Initiated Seed		Seed Set		% abortion
	Mean ¹	SD	Mean ²	SD	
P1	2.545 ^a	2.186	1.373 ^A	3.553	46.1
P2	2.675 ^b	2.428	1.568 ^B	3.922	41.4
P3	2.385 ^c	1.290	1.520 ^B	2.926	36.3

¹ Means followed by the same letter did not differ, by Mann-Whitney comparisons, P1xP2, $c^2=6.65$, $p=0.010$, $df=1$; P1xP3, $c^2=7.49$, $p=0.006$, $df=1$; P2xP3, $c^2=30.62$, $p<0.001$, $df=1$.

² Means followed by the same letter did not differ, by Mann-Whitney comparisons, P1xP2, $c^2=9.36$, $p=0.002$, $df=1$; P1xP3, $c^2=14.43$, $p<0.001$, $df=1$; P2xP3, $c^2=0.113$, $p=0.737$, $df=1$.

TABLE 3

Mean number of initiated seed per fruit and standard deviation, for *T. semitriloba*, in each patch and flowering month.

Patch	March		April		May	
	Mean	SD	Mean	SD	Mean	SD
P1 ¹	3.008a	0.873	2.364b	0.755	2.264b	0.924
P2 ²	3.172c	0.960	2.468d	0.787	2.384d	0.942
P3 ³	2.580e	0.604	2.352f	0.624	2.224f	0.732

¹ Means followed by the same letter did not differ, by Mann-Whitney comparisons; March x April, $c^2=75.47$, d.f.=1, $p<0.001$; March x May, $c^2=78.29$, d.f.=1, $p<0.001$; April x May, $c^2=1.82$, d.f.=1, $p=0.177$.

² Means followed by the same letter did not differ, by Mann-Whitney comparisons; March x April, $c^2=75.40$, d.f.=1, $p<0.001$; March x May, $c^2=74.56$, d.f.=1, $p<0.001$; April x May, $c^2=0.79$, d.f.=1, $p=0.795$.

³ Means followed by the same letter did not differ, by Mann-Whitney comparisons; March x April, $c^2=18.22$, d.f.=1, $p<0.001$; March x May, $c^2=31.78$, d.f.=1, $p<0.001$; April x May, $c^2=3.32$, d.f.=1, $p=0.068$.

TABLE 4

Mean seed set per fruit, standard deviation, and proportion of seed abortion, for *T. semitriloba*, in each patch and flowering month.

Patch	March			April			May		
	Mean	SD	% Ab ⁴	Mean	SD	% Ab ⁴	Mean	SD	% Ab ⁴
P1 ¹	1.520 ^a	1.213	49.5	1.052 ^b	0.970	55.5	1.548 ^a	1.068	31.6
P2 ²	1.864 ^c	1.310	41.2	1.128 ^d	1.026	54.3	1.712 ^c	1.074	28.2
P3 ³	1.684 ^c	0.841	40.6	1.560 ^e	0.868	33.7	1.316 ^f	0.914	40.8

¹ Means followed by the same letter did not differ, by Mann-Whitney comparisons; March x April, $c^2=17.89$, d.f.=1, $p<0.001$; March x May, $c^2=0.56$, d.f.=1, $p=0.456$; April x May, $c^2=27.29$, d.f.=1, $p<0.001$.

² Means followed by the same letter did not differ, by Mann-Whitney comparisons; March x April, $c^2=40.59$, d.f.=1, $p<0.001$; March x May, $c^2=0.75$, d.f.=1, $p=0.386$; April x May, $c^2=36.96$, d.f.=1, $p<0.001$.

³ Means followed by the same letter did not differ, by Mann-Whitney comparisons; March x April, $c^2=2.36$, d.f.=1, $p=0.125$; March x May, $c^2=20.93$, d.f.=1, $p<0.001$; April x May, $c^2=9.56$, d.f.=1, $p=0.002$.

⁴ Pearson's Chi-Square comparisons for proportion of seed abortion between month, within patches. P1: $c^2=22.59$, d.f.=2; P2: $c^2=15.84$, d.f.=2, $c^2=3.26$, d.f.=2.

Spatial (among patches) and temporal (among flowering months) variation on seed initiation and seed set was analyzed with a Kruskal-Wallis non-parametric ANOVA. Mean number of initiated seed per fruit and mean seed set were compared by a Mann-Whitney test, according to hypothesis evaluated. Proportion of seed abortion was analyzed by Pearson's Chi-square considering $p=0.05$, comparing observed frequencies among patches and flowering months, with the expected for equal frequencies.

RESULTS

Seed initiation and seed set was low: mean seed initiation and seed set, pooling all patches and flowering months were 2.535 (sd=0.145) and 1.487 (sd=0.102), respectively, although maximum number could reach six seeds per fruit. This resulted in a mean seed abortion of 41.3%.

There was a significant patch effect on seed initiation and seed set, pooling all flowering months (seed initiation, $N=2250$, $df=2$, $U=29.621$, $p<0.001$; seed set, $N=2250$, $df=2$, $U=15.887$, $p<0.001$). Patch P2 initiated more seeds than P1 and P3, but in P2 and P3 seed set was higher than in P1 (Table 2).

For temporal variation, data of each patch were analyzed separately, due to differences in seed initiation and seed set among patches. There was a significant effect of flowering month on seed initiation and on seed set, in all patches: (initiated seeds - P1, $U=102.924$, $p<0.001$; P2, $U=100,336$, $p<0.001$; P3, $U=35.138$, $p<0.001$; seed set - P1, $U=30.353$, $p<0.001$; P2, $U=51,992$, $p<0.001$; P3, $U=29.988$, $p<0.001$; $N=750$ and $df=2$ for all cases). Seed initiation was higher in the first flowering month (March, Table 3), for all patches. Seed set per fruit was lower in the second flowering month (April), for P1 and P2, but did not differ from the first month for P3

(Table 4).

The proportion of seed abortion did not differ among patches, pooling all months ($c^2=7.1$, d.f.=2, Table 3). A temporal variation of seed abortion occurred in P1 and P2 (Table 4). The proportion of seed abortion was higher in the second month (April) - but not for P3 (Table 4).

DISCUSSION

The observed spatial pattern in reproductive success was probably due to spatial heterogeneity in patch "quality", such as nutrient and water availability, and by differences in pollinator service (Haig and Westoby 1988, Hendrix 1988).

Patch P1 was situated on a hill and plants were submitted to water stress during dry season (May to September), losing almost all leaves. Therefore, a large part of metabolites might be allocated for leaf growth in the summer, before flowering. Patch P2 was localized along a river-side and plants were not submitted to an intense water stress, such as plants in P1 (there was no leaf fall), hence more resources might be allocated to reproduction. Plants in P3, situated in a forest trail, were not submitted to water stress, but to low light intensity, causing etiolation and leaf enlargement. Probably, on this patch resource allocation for vegetative structure and biomass maintenance was higher than on the other patches. These differences could have resulted in a higher production of flowers in P2 (Collevatti 1995).

Patches with higher density of flowers may attract more bees, resulting in a higher rate of cross-pollination (Stephenson 1982, Pyke 1984, Zimmerman 1987). This might result in the higher initiation of seeds and seed set in P2 and the lower number of initiated seeds in P3. In fact, the greater brood size on P2 was not due to spatial variability in seed abortion. Proportion of seed abortion did not differ between patches, but patch "quality", number of flowers per plant and abundance of pollinators were quite different (Collevatti 1995).

Temporal pattern in reproductive success was similar in patches P1 and P2, with a higher initiation of seeds on the first flowering month, and higher seed set in the first and last flowering months (March and May). The number of

flowers on a plant may influence pollinator behavior, and ultimately, outcrossing rate and seed set (Stephenson 1982, Zimmerman 1987, Vaughton 1990b). Pollinators tend to stay on plants with more flowers (Pyke 1984), increasing self-pollination. Plant species in which flower production varies along flowering season may experience a difference in pollinator service. In the peak of flowering phase, individuals are more conspicuous and more visited, but outcrossing rate is lower due to higher residence time. In the first and last phases, outcrossing rate is higher due to a higher frequency of movement between plants (Stephenson 1982, Augspurger 1980, Vaughton 1990b). In March and May, the number of flowers per plant tended to be lower in *T. semitriloba* (Collevatti 1995), hence, residence time of pollinators might be lower, increasing outcrossing rate and consequently seed viability. Moreover, proportion of seed abortion was higher in the second month (month with greater number of flowers per plant, and probably when self-pollination was higher).

Patch P3, a high "quality" patch, but with lower number of flowers per plant, had a different temporal pattern. Although number of initiated seeds was higher on the first month, such as P1 and P2, seed set was higher in the first and second months, and seed abortion did not differ. Temporal pattern of seed set followed temporal pattern of flower production (Collevatti 1995). We hypothesized that on this patch, seed set was not correlated to outcrossing rate but with pollinator abundance and behavior. The low abundance of pollinators could cause a limitation of pollen resulting in a lower initiation of seeds and seed set (Murali 1993). During the last flowering month, the number of flowers per plant and number of bee pollinator was quite lower (compared to the other patches or to the other months in the same patch), and flowering season finished earlier in this patch than in the others (Collevatti 1995). Additionally, flowers were intensively consumed by two species of beetles, *Pseudodiabrotica* spp. (Coleoptera: Chrysomelidae) which could result in lower seed set, due to herbivory (Vaughton 1990a, Hendrix 1988).

Our results showed that *T. semitriloba* may experience a spatial and temporal variability in reproductive success. This pattern is expected

for a weed species, which may colonize different patches, leading to a spatial imprevisibility in nutrient availability and pollinator service (among patch variation in pollinator abundance and species composition). Temporal variability may be caused by differences in environmental favorability among flowering months. Since flowering season is long (three months), this species may experience temporal heterogeneity in pollinator service, depletion of soil nutrients and nutritional reserves, and differences on genetic quality between siblings generating opportunities for sibling rivalry, and for mate choice or gamete selection (Shaanker *et al.* 1988, Joshi, Shankar and Ganeshaiyah 1993, O'Donnell and Bawa 1993).

ACKNOWLEDGMENTS

This study was developed during the MSc. program of the first author, and was supported by the Universidade Federal de Viçosa and a grant from CAPES, whose assistance we gratefully acknowledge. We thank Lúcio A.O. Campos, José H.Schoederer and Alexandre F. da Silva for suggestions, Maria do Carmo Vieira for field and laboratory assistance and John D. Hay and an anonymous referee for helpful comments on the manuscript.

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