Temporal patterns of flowering and pod-set among *Theobroma* and *Herrania* species in a Costa Rican garden plot

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The number of floral buds, open flowers, inflorescences, and fruits (pods) were recorded at varying intervals over several years in a Costa Rican garden plot with mature trees of two species from the genus *Theobroma* (*T, simiarum, T. speciosum)* and three species from the genus *Herrania* (*H. albiflora, H. nitida and H. purpurea*) (Malvaceae: Byttnerioideae). While there were considerable differences in the number of flowers, inflorescences and open flowers, timing of these outputs only significantly differed in the timing of pod production; in this respect the species fell into roughly two groups though these groups did not correspond to the two genera. *H. albiflora, H. purpurea,* and *T. speciosum* all produced more pods in December, February, and March. Alternatively, *H. nitida* and *T. simiarum* produced more pods in September. This paper adds to our knowledge of how closely related species in the same habitat partition the timing of flowering and pod-set.

Keywords: Costa Rica, flowering, herrania, pod production, seasonality, theobroma

Theobroma cacao L. is well-known as the world's principal source of cocoa and chocolate, having been cultivated over the millennia (Coe and Coe 1996; McNeil 2006; Young 1994). Several other species of *Theobroma* such as *T. bicolor*, *I. grandiflorum*, and the closely related genus *Herrania* (Whitlock and Baum 1999) are considered potential sources of economically relevant products, including chocolate. Some of these species have been cultivated on a small scale in garden plots in South America (Aguiar-Falcas and Lieras 1983; Balée 1989; Encinas Dardengo et al. 2018). In spite of this potential interest, natural history and ecological studies of these species are lacking.

The closely related genera of *Theobroma* and *Herrania* (Malvaceae: Byttnerioideae) are endemic to the Neotropics, with their highest number of species occurring in the Amazon basin (Cuatrecasas 1964). The most well-known species of *Theobroma* is *T. cacao*, the world's principal source of commercial cocoa and chocolate (Young 1994). While native to both Central and South America, *T. cacao* occurs in Central America along with *T. speciosum* Willd. ex Spreng., *T. bicolor* Bonpl., *T. simiarum* Donn. Sm., *H. purpurea* (Pittier) R.E. Schult., and others (Standley 1937). Among the many species of *Theobroma*, there are greatly different patterns of flowering. For example, *T. cacao* tends to dribble out a few flowers over several months in the forest habitat of Manu National Park in Peru as contrasted with the explosive bursts of flowering in *T. speciosum* in the same habitat (C.H. Janson, pers. comm., Feb. 1983). Cultivated *T. cacao* typically produces prodigious numbers of flowers seasonally in Central America (Young 1983; 1984; 1987). Due to co-occurrence of several species in both genera in forest habitats, strong selection for phenological differences in pod (fruit) production might be expected, especially if species share common dispersal agents (Janson 1983). Also, if species share common pollinators, we might expect that flowering and therefore podset are similarly timed (Chen and Hsu 2011). This type of synchronous flowering and podset may enhanced pollination efficiency (Satake and Iwasa 2000) and increase seed and seedling survival due to seed

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predator satiation (Janzen 1974).

In this paper, we summarize a multi-year study of the temporal patterns of flower and fruit (pod) production for several species of *Theobroma* and *Herrania* in a garden planting in Costa Rica, one of the few studies of its kind for these genera. The data presented in this paper represent one of the first accounts of flowering and pod production in a mixed-species garden plot. These findings have implications for the annual patterns of fruit availability for potential seed dispersal agents (Janson 1983). Our study examines the hypothesis that these closely related species may have distinct temporal patterns of reproductive behavior. The results suggest patterns of availability of pods on an annual basis among these species for potential economic uses by local communities in the Neotropics. They also provide an impetus for further studies.

Materials and methods

This study was conducted over a five-year period (1981-1986) in “Finca Experimental La Lola” (hereafter “La Lola”) near Siquirres (10°06’ N, 83°30’ W), Limon province, elevation 50m, Costa Rica. This region, within lowland tropical wet forest (Holdridge 1967), tends to have heavy monthly rainfall throughout the year (Figure 1). While La Lola is a several-hundred hectare cultivated cacao farm, it also contains a small garden plot of several species of *Theobroma* and *Herrania* native to Central America and/or South America. There were five species present: *T. speciosum* (six individuals*); T. simiarum* (three individuals)*; H. purpurea* (22 individuals*); H. nitida* Poepp. R.E. Schult. (two individuals) and *H. albiflora* Goudot (five individuals). This garden-type plot consisted of a single row of several trees for each of five species for a total of five parallel rows. The trees were most likely planted from seed in the 1960s as a demonstration plot. Unlike the surrounding acres of *Theobroma cacao*, these trees are wild types. The garden was bordered on one side by a gravel road, two other sides in *T. cacao*, and the fourth side by a small grove of *T. mammosum* Cuatrec and J. León trees. Rainfall data was recorded on a rain gauge located on the premises.

Given that these several species were present in the same garden, there was the unique opportunity to assess the possible differences in flowering and fruit production among them. Although the trees sampled varied in size and branching structure, thereby influencing the floral and pod comparative data, the results could still reveal whether at the time of sampling they differ in flowering and fruiting patterns. *Theobroma cacao*, although very abundant at this site, was excluded from the study because it is a cultivar (many) rather than in a wild state. Data were collected by exhaustively counting all inflorescences, floral buds, and open flowers within inflorescences and fruits (pods) greater than 2 cm in length but did not include aborted cherelles on 22 occasions over 5 years.

Inflorescences and flowers on pods were counted on trunks and branches on all trees. All trees were counted on each observation date. However, not all trees were in flowering, budding, or podding at a given observation date. These non-flowering, budding, podding trees were measured as zero (Table 1). For trees more than 3 meters tall, such as *T. simiarum*, visual estimates from the ground were made on flowers and pods in the canopy. The ages of individual trees were not known. Checking with personnel at CATIE (Centro Tropico de Investigación y Enseñanza) in Turrialba, the overseers of La Lola, failed to provide dates as to when the trees were established. All size classes of pods were counted.

Because the dataset contained so many measured zeros, rather than using the total number of instances of a given category, the proportion of each category was calculated (i.e. inflorescence, flower, fruit) as the total number at a given collection date divided by the total number in a category during a given year. The data were analysed in R using mixed effects analysis of variance with the package lme4 (Bates et al. 2015), with lmerTest (Kuznetsova et al. 2017) to produce Satterwaithe approximations of denominator degrees of freedom. Proportions of inflorescences, buds, flowers and pods were calculated as the number counted in a given month in a given year divided by the total number counted for that species in a given year (Figures 2 – 5).

Month was treated as a categorical variable in this analysis because data were not collected continuously throughout the year but rather during specific months. Figures were produced in the package "ggplot2" (Wickham 2009) and tables were produced in the package "knitr" (Xie 2019).

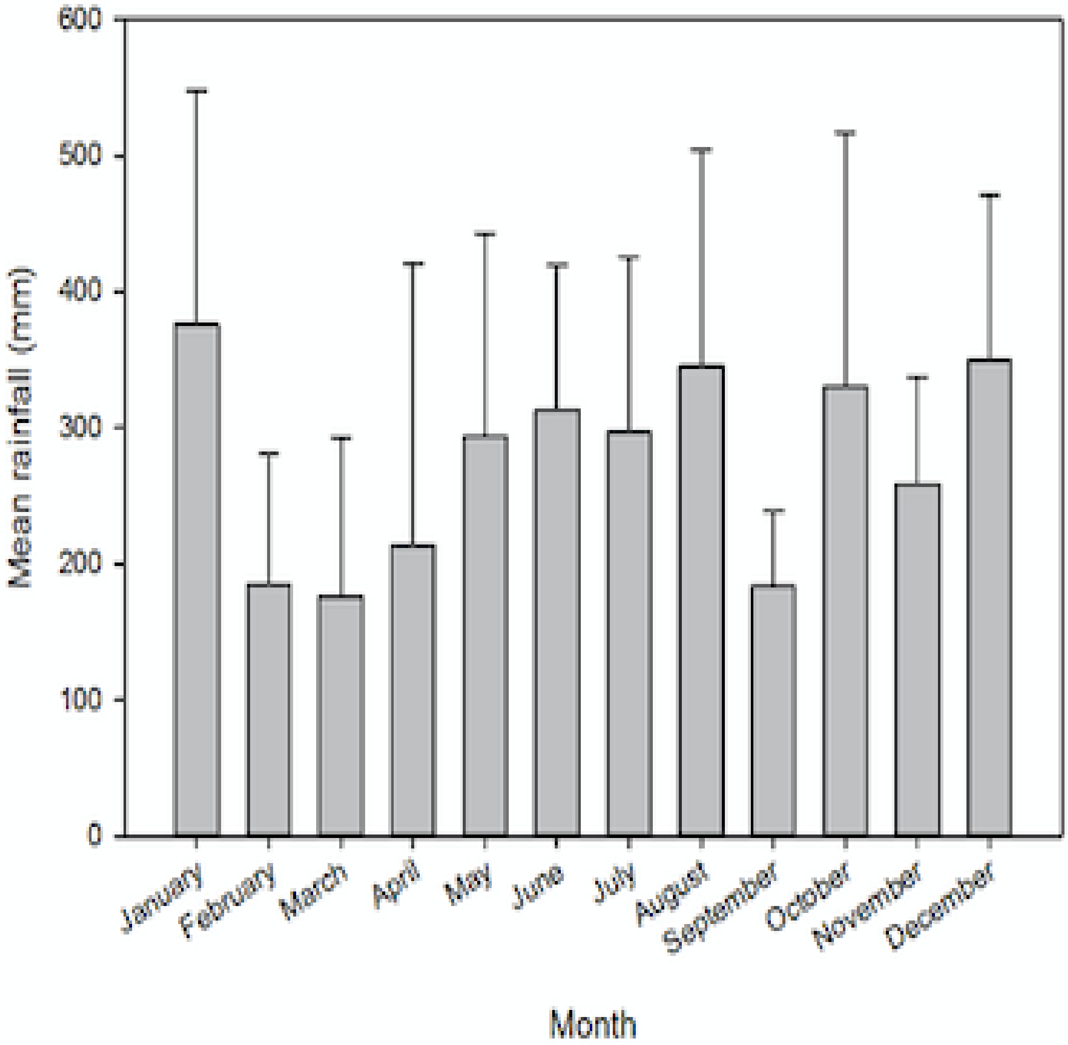

Figure 1: Rainfall data for Finca Experimental La Lola, near Siquirres, Limon Province, Costa Rica expressed as monthly means (bars) with standard deviations (lines) for 1984-1990.

Table 1: General data summary with the number of inflorescences, buds, open flowers, and pods in each month in each sampling year as well as the number of trees that exhibited the phenological stage (trees counted) for that species at that observation time and the total number of trees in the common garden for each species

Species	**Month**	**Year**	**Inflorescences**	**Buds**	**Open flowers**	**Pods**	**Trees counted**	**Total # Trees**
H. albiflora	Dec	82	300	85	8	48	1	5
H. albiflora	Feb	83	29	9	0	49	5	5
H. albiflora	Jul	83	1164	315	5	124	5	5
H. albiflora	Oct	83	767	24	13	263	5	5
H. albiflora	Aug	84	440	100	19	136	5	5
H. albiflora	Mar	84	1912	13	7	1046	5	5
H. albiflora	Mar	85	1687	3	5	949	5	5
H. albiflora	Sep	85	15	5	1	35	5	5
H. albiflora	Dec	86	12	0	0	35	4	5
H. albiflora	Feb	86	3523	276	27	590	5	5
H. albiflora	Jul	86	378	93	7	68	5	5
H. albiflora	Feb	87	1214	62	8	345	4	5
H. albiflora	Jul	87	70	6	0	158	4	5
H. albiflora	Feb	88	154	48	4	96	3	5
H. albiflora	Jun	88	16	0	0	41	3	5
H. albiflora	Sep	89	0	0	0	6	3	5
H. albiflora	Feb	89	0	0	0	2	1	5
H. albiflora	Jun	90	0	0	0	32	2	5
H. nitida	Jul	83	112	49	26	38	1	2
H. nitida	Oct	83	3	3	3	6	2	2
H. nitida	Mar	83	231	107	2	42	1	2
H. nitida	Aug	84	152	147	43	48	1	2
H. nitida	Mar	84	771	598	1	106	1	2
H. nitida	Mar	85	105	88	5	28	1	2
H. nitida	Sep	85	490	345	30	86	1	2
H. nitida	Dec	86	378	493	0	54	1	2
H. nitida	Feb	86	78	22	14	24	1	2
H. nitida	Jul	86	120	60	13	30	1	2
H. nitida	Jul	87	276	166	7	48	1	2
H. nitida	Feb	87	78	47	0	28	1	2
H. nitida	Feb	88	0	0	0	2	1	2
H. nitida	Jun	88	0	0	0	2	1	2
H. nitida	Sep	88	153	26	26	36	1	2
H. nitida	Feb	89	0	0	0	2	1	2
H. purpurea	Dec	82	915	247	17	523	21	22
H. purpurea	Jul	83	1239	527	81	1025	20	22
H. purpurea	Oct	83	1010	396	39	931	20	22
H. purpurea	Feb	83	1346	40	1	1055	20	22
H. purpurea	Aug	84	595	170	5	387	22	22
H. purpurea	Mar	84	11867	48	9	5684	22	22
H. purpurea	Mar	85	12384	138	0	6342	21	22
H. purpurea	Dec	86	914	1764	0	262	18	22
H. purpurea	Jul	86	341	75	45	233	14	22
H. purpurea	Feb	86	9651	354	54	2170	17	22
H. purpurea	Feb	87	1515	31	0	1575	16	22

Table 1 continued: General data summary with the number of inflorescences, buds, open flowers, and pods in each month in each sampling year as well as the number of trees that exhibited the phenological stage (trees counted) for that species at that observation time and the total number of trees in the common garden for each species

Species	**Month**	**Year**	**Inflorescences**	**Buds**	**Open flowers**	**Pods**	**Trees counted**	**Total # Trees**
H. purpurea	Jul	87	198	0	0	355	16	22
H. purpurea	Jun	88	9	0	0	112	13	22
H. purpurea	Sep	88	68	14	7	205	20	22
H. purpurea	Feb	88	332	102	3	235	14	22
H. purpurea	Feb	89	172	28	3	85	6	22
H. purpurea	Sep	89	13	0	0	91	8	22
H. purpurea	Mar	90	0	0	0	2	1	22
H. purpurea	Jun	90	6	0	0	115	6	22
H. purpurea	Feb	91	0	0	0	4	2	22
T. simiarum	Dec	82	649	1500	0	122	3	3
T. simiarum	Oct	83	1203	891	55	156	3	3
T. simiarum	Mar	83	1410	557	128	185	3	3
T. simiarum	Jul	83	105	93	0	79	3	3
T. simiarum	Aug	84	2764	1082	64	244	3	3
T. simiarum	Mar	84	5015	2880	268	368	3	3
T. simiarum	Mar	85	4105	2487	191	384	3	3
T. simiarum	Feb	86	6413	5487	225	414	3	3
T. simiarum	Dec	86	90	5587	254	53	2	3
T. simiarum	Jul	86	198	0	0	188	2	3
T. simiarum	Feb	87	1073	1307	21	188	3	3
T. simiarum	Jul	87	1012	737	7	158	2	3
T. simiarum	Feb	88	6	15	3	6	1	3
T. simiarum	Sep	88	7582	3980	64	416	3	3
T. simiarum	Sep	89	1784	2301	186	122	2	3
T. speciosum	Dec	82	254	51	179	46	2	6
T. speciosum	Feb	83	1992	2291	717	261	3	6
T. speciosum	Jul	83	319	61	224	206	4	6
T. speciosum	Oct	83	3	0	0	74	4	6
T. speciosum	Mar	84	1369	1958	442	235	4	6
T. speciosum	Aug	84	155	479	145	87	4	6
T. speciosum	Mar	85	946	695	545	92	3	6
T. speciosum	Feb	86	2418	12596	127	285	5	6
T. speciosum	Dec	86	0	777	171	80	5	6
T. speciosum	Jul	86	6	0	0	20	4	6
T. speciosum	Jul	87	284	323	666	0	5	6
T. speciosum	Feb	87	0	0	31	110	4	6
T. speciosum	Feb	88	1	0	0	5	1	6
T. speciosum	Sep	88	0	0	0	8	4	6
T. speciosum	Sep	89	497	1571	544	64	2	6
T. speciosum	Feb	89	408	1872	81	137	5	6

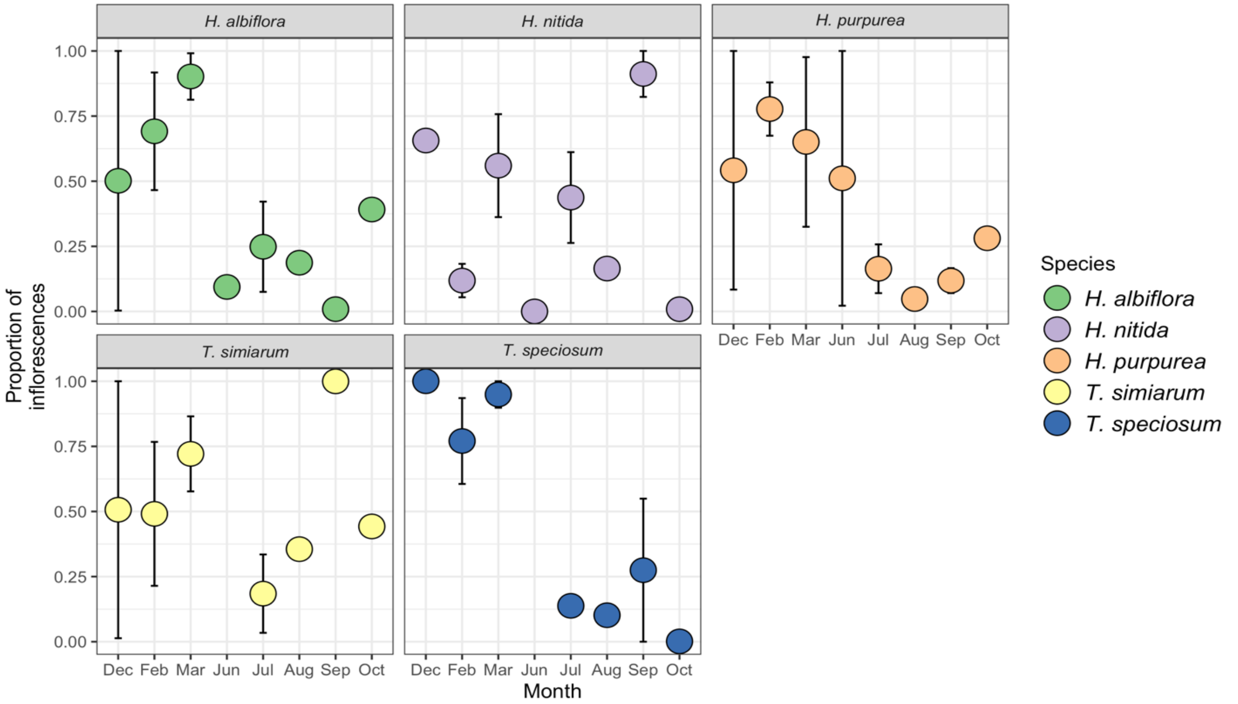

Figure 2: Timing of inflorescence across the year. Proportion of inflorescences is calculated as the number of counted inflorescences in a given month in a given year divided by the total number of inflorescences counted for that species in a given year. Error bars represent standard error.

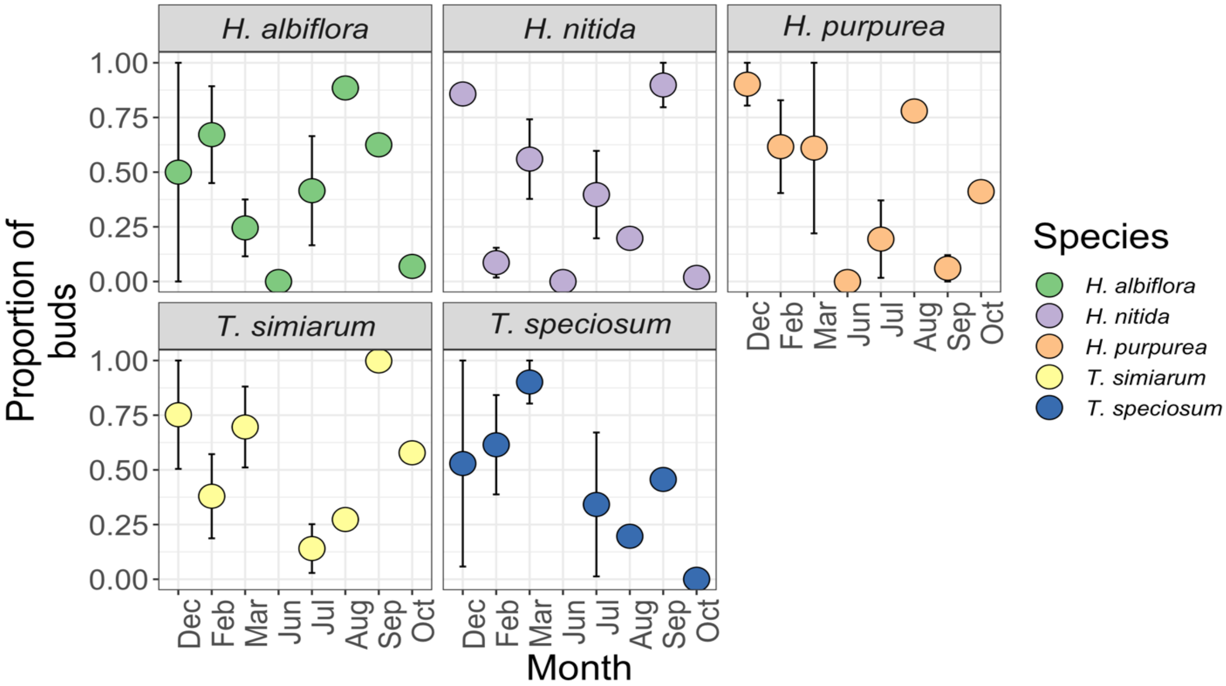

Figure 3: Timing of budding across the year. Proportion of buds is calculated as the number of counted buds in a given month in a given year divided by the total number of buds counted for that species in a given year. Error bars represent standard error.

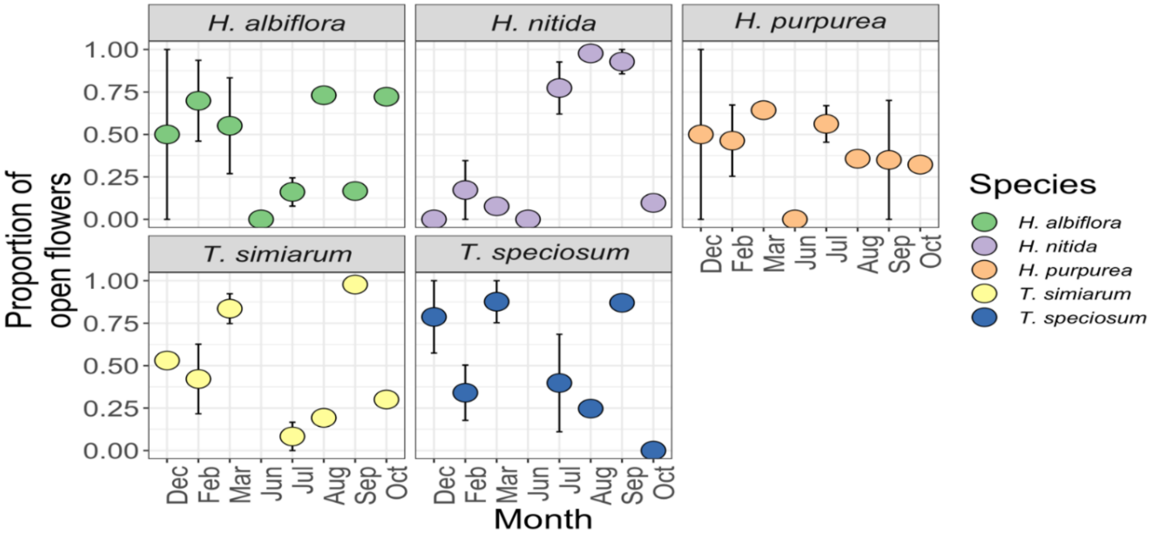

Figure 4: Timing of flower opening across the year. Proportion of open flowers is calculated as the number of counted open flowers in a given month in a given year divided by the total number of open flowers counted for that species in a given year. Error bars represent standard error.

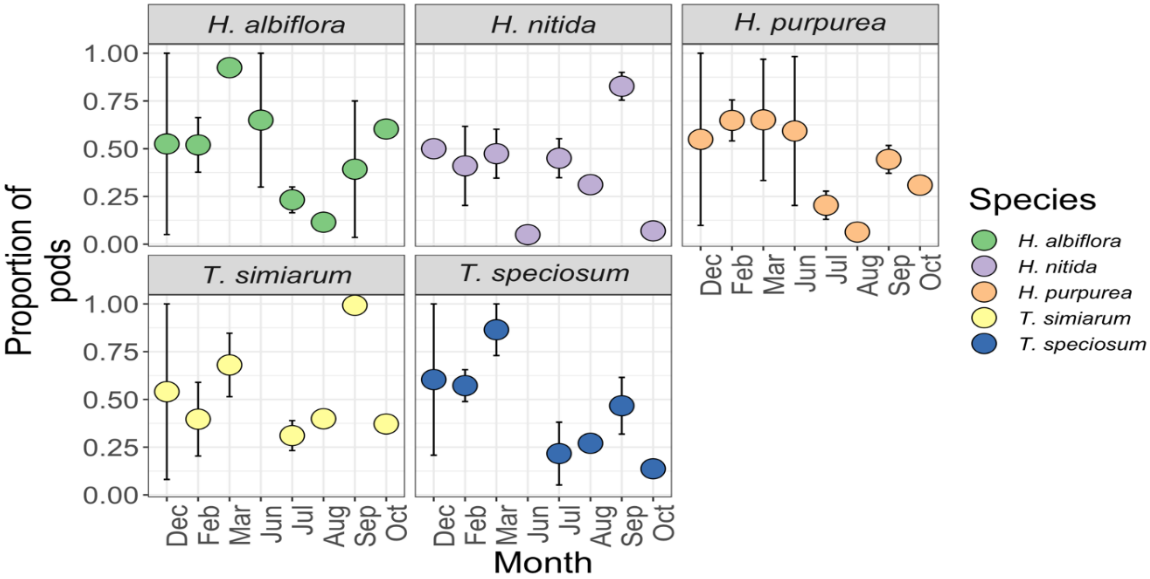

Figure 5: Timing of podding across the year. Proportion of pods is calculated as the number of counted pods in a given month in a given year divided by the total number of pods counted for that species in a given year. Error bars represent standard error.

Results

Although the number of trees studied was small, these data are presumably the first known phenological study of these tree species and therefore worth documenting. Given these limitations, we found that species differed significantly in the total number of inflorescences ($F_{4,33} = 3.21$, $P = 0.025$, Table 2 and Figure 2), buds ($F_{4,44} = 2.601$, $P = 0.049$, Table 3 and Figure 3), open flowers ($F_{4,47} = 5.942$, $P = 0.001$, Table 4 and Figure 4) and fruit pods ($F_{4, 35} = 6.892$, $P < 0.001$, Table 5 and Figure 5).

However, the timing of this output was only significantly different in terms of the timing of fruit pods ($F_{26,35} = 2.800$, $P = 0.002$, Table 5 and Figure 5). That is, these species of

Theobroma and *Herrania* had similarly timed proportions of inflorescences, buds, and open flowers but had fruit pods during different months of observation. The species fell into roughly two groups, *Herrania purpurea*, *Theobroma speciosum*, and *Herrania albiflora* produced more pods in December, February, and March. Alternatively, *Herrania nitida* and *Theobroma simiarum* produced more pods in September (Table 5).

Table 2: Data presented in Figure 2 – proportion of total inflorescences across time. Proportion of total inflorescences is calculated as the number of inflorescences counted in a month divided by the total number of inflorescences counted in that year. N represents the number of trees with inflorescences at the given observation time step for the species

Species	Month	N	Proportion of total inflorescences	Standard error
H. albiflora	Feb	4	0.692	0.226
H. albiflora	Mar	2	0.902	0.089
H. albiflora	Jun	1	0.094	NA
H. albiflora	Jul	3	0.248	0.173
H. albiflora	Aug	1	0.187	NA
H. albiflora	Sep	1	0.009	NA
H. albiflora	Oct	1	0.391	NA
H. albiflora	Dec	2	0.502	0.498
H. nitida	Feb	3	0.119	0.064
H. nitida	Mar	3	0.560	0.198
H. nitida	Jun	1	0.000	NA
H. nitida	Jul	3	0.437	0.174
H. nitida	Aug	1	0.165	NA
H. nitida	Sep	2	0.912	0.088
H. nitida	Oct	1	0.009	NA
H. nitida	Dec	1	0.656	NA
H. purpurea	Feb	5	0.777	0.102
H. purpurea	Mar	3	0.651	0.326
H. purpurea	Jun	2	0.511	0.489
H. purpurea	Jul	3	0.164	0.094
H. purpurea	Aug	1	0.048	NA
H. purpurea	Sep	2	0.118	0.048
H. purpurea	Oct	1	0.281	NA
H. purpurea	Dec	2	0.542	0.458
T. simiarum	Feb	3	0.491	0.276
T. simiarum	Mar	3	0.721	0.144
T. simiarum	Jul	3	0.185	0.150
T. simiarum	Aug	1	0.355	NA
T. simiarum	Sep	2	1.000	0.000
T. simiarum	Oct	1	0.443	NA
T. simiarum	Dec	2	0.507	0.493
T. speciosum	Feb	3	0.771	0.165
T. speciosum	Mar	2	0.949	0.051
T. speciosum	Jul	1	0.138	NA
T. speciosum	Aug	1	0.102	NA
T. speciosum	Sep	2	0.275	0.275
T. speciosum	Oct	1	0.001	NA
T. speciosum	Dec	1	1.000	NA

Table 3: Data presented in Figure 3 – proportion of total buds across time. Proportion of total buds is calculated as the number of buds counted in a month divided by the total number of buds counted in that year. N represents the number of trees with buds at the given observation time for the species

Species	Month	N	Proportion of total buds	Standard error
H. albiflora	Feb	4	0.671	0.221
H. albiflora	Mar	2	0.245	0.130
H. albiflora	Jun	1	0.000	NA
H. albiflora	Jul	3	0.415	0.250
H. albiflora	Aug	1	0.885	NA
H. albiflora	Sep	1	0.625	NA
H. albiflora	Oct	1	0.069	NA
H. albiflora	Dec	2	0.500	0.500
H. nitida	Feb	3	0.086	0.068
H. nitida	Mar	3	0.560	0.182
H. nitida	Jun	1	0.000	NA
H. nitida	Jul	3	0.397	0.200
H. nitida	Aug	1	0.197	NA
H. nitida	Sep	2	0.898	0.102
H. nitida	Oct	1	0.019	NA
H. nitida	Dec	1	0.857	NA
H. purpurea	Feb	5	0.616	0.212
H. purpurea	Mar	2	0.610	0.390
H. purpurea	Jun	1	0.000	NA
H. purpurea	Jul	3	0.194	0.177
H. purpurea	Aug	1	0.780	NA
H. purpurea	Sep	2	0.060	0.060
H. purpurea	Oct	1	0.411	NA
H. purpurea	Dec	2	0.902	0.098
T. simiarum	Feb	3	0.380	0.192
T. simiarum	Mar	3	0.696	0.185
T. simiarum	Jul	3	0.140	0.112
T. simiarum	Aug	1	0.273	NA
T. simiarum	Sep	2	0.998	0.002
T. simiarum	Oct	1	0.578	NA
T. simiarum	Dec	2	0.752	0.248
T. speciosum	Feb	4	0.615	0.227
T. speciosum	Mar	2	0.902	0.098
T. speciosum	Jul	3	0.342	0.329
T. speciosum	Aug	1	0.197	NA
T. speciosum	Sep	1	0.456	NA
T. speciosum	Oct	1	0.000	NA
T. speciosum	Dec	2	0.529	0.471

Table 4: Data presented in Figure 4 – proportion of total open flowers across time. Proportion of total open flowers is calculated as the number of open flowers counted in a month divided by the total number of open flowers counted in that year. N represents the number of trees with open flowers at the given observation time for the species

Species	Month	N	Proportion of total open flowers	Standard error
H. albiflora	Feb	4	0.699	0.238
H. albiflora	Mar	2	0.551	0.282
H. albiflora	Jun	1	0.000	NA
H. albiflora	Jul	3	0.161	0.083
H. albiflora	Aug	1	0.731	NA
H. albiflora	Sep	1	0.167	NA
H. albiflora	Oct	1	0.722	NA
H. albiflora	Dec	2	0.500	0.500
H. nitida	Feb	3	0.173	0.173
H. nitida	Mar	3	0.077	0.035
H. nitida	Jun	1	0.000	NA
H. nitida	Jul	3	0.773	0.153
H. nitida	Aug	1	0.977	NA
H. nitida	Sep	2	0.929	0.071
H. nitida	Oct	1	0.097	NA
H. nitida	Dec	1	0.000	NA
H. purpurea	Feb	4	0.463	0.210
H. purpurea	Mar	1	0.643	NA
H. purpurea	Jun	1	0.000	NA
H. purpurea	Jul	2	0.562	0.107
H. purpurea	Aug	1	0.357	NA
H. purpurea	Sep	2	0.350	0.350
H. purpurea	Oct	1	0.322	NA
H. purpurea	Dec	2	0.500	0.500
T. simiarum	Feb	3	0.422	0.205
T. simiarum	Mar	3	0.836	0.088
T. simiarum	Jul	3	0.083	0.083
T. simiarum	Aug	1	0.193	NA
T. simiarum	Sep	2	0.978	0.022
T. simiarum	Oct	1	0.301	NA
T. simiarum	Dec	1	0.530	NA
T. speciosum	Feb	4	0.341	0.163
T. speciosum	Mar	2	0.876	0.124
T. speciosum	Jul	3	0.398	0.287
T. speciosum	Aug	1	0.247	NA
T. speciosum	Sep	1	0.870	NA
T. speciosum	Oct	1	0.000	NA
T. speciosum	Dec	2	0.787	0.213

Table 5: Data presented in Figure 5 – proportion of total pods across time. Proportion of total pods is calculated as the number of pods counted in a month divided by the total number of pods counted in that year. N represents the number of trees with pods at the given observation time for the species

Species	Month	N	Proportion of total pods	Standard error
H. albiflora	Feb	5	0.520	0.143
H. albiflora	Mar	2	0.925	0.040
H. albiflora	Jun	2	0.650	0.350
H. albiflora	Jul	3	0.232	0.068
H. albiflora	Aug	1	0.115	NA
H. albiflora	Sep	2	0.393	0.357
H. albiflora	Oct	1	0.603	NA
H. albiflora	Dec	2	0.525	0.475
H. nitida	Feb	4	0.410	0.207
H. nitida	Mar	3	0.474	0.128
H. nitida	Jun	1	0.050	NA
H. nitida	Jul	3	0.450	0.102
H. nitida	Aug	1	0.312	NA
H. nitida	Sep	2	0.827	0.073
H. nitida	Oct	1	0.070	NA
H. nitida	Dec	1	0.500	NA
H. purpurea	Feb	6	0.648	0.107
H. purpurea	Mar	3	0.651	0.318
H. purpurea	Jun	2	0.593	0.390
H. purpurea	Jul	3	0.204	0.074
H. purpurea	Aug	1	0.064	NA
H. purpurea	Sep	2	0.444	0.073
H. purpurea	Oct	1	0.309	NA
H. purpurea	Dec	2	0.549	0.451
T. simiarum	Feb	3	0.397	0.193
T. simiarum	Mar	3	0.681	0.166
T. simiarum	Jul	3	0.311	0.078
T. simiarum	Aug	1	0.399	NA
T. simiarum	Sep	2	0.993	0.007
T. simiarum	Oct	1	0.371	NA
T. simiarum	Dec	2	0.540	0.460
T. speciosum	Feb	4	0.572	0.083
T. speciosum	Mar	2	0.865	0.135
T. speciosum	Jul	2	0.216	0.164
T. speciosum	Aug	1	0.270	NA
T. speciosum	Sep	2	0.467	0.148
T. speciosum	Oct	1	0.137	NA
T. speciosum	Dec	2	0.604	0.396

Discussion

It is not uncommon in Neotropical forests for related species to have considerable differences in the timing of fruit production (Janson 1983; Milton 1991). Our data demonstrate that closely related species can differ greatly in the levels of fruit production at specific times of the year in spite of similar flowering time in these two closely related tropical genera. The timing of fruit production varied greatly among the genera and species in this garden plot in spite of their similar planting environment. However, note that these observations were made in a very humid location and may not be broadly applicable across different climatic regions.

For indigenous peoples tending garden plots containing these tree species, it may therefore be possible to have yields of fruit (albeit in relatively small numbers) at several time points in the year with month-to-month differences in the species of fruit available for possible use. Such yields could vary greatly among different localities. Further, these species in combination may allow for two larger harvest times, December through March and September through October, again depending on locality. However, the use of polycultures like these for commercial sale is likely limited. These species are less commercially viable than *T. cacao* which, when domesticated can produce cacao year-round.

Planting these species in polyculture with *T. cacao* may increase resistance to disease for *T. cacao.* Given the many agronomic challenges concerning pest diseases associated with commercially-grown *T. cacao* (Avelino et al. 2011; Ratnadass et al. 2012; Pumarino et al. 2015), there is a potential benefit of genetic studies of resistance in various species of *Theobroma* and *Herrania* such as these for *T. cacao* (Whitlock and Baum 1999; Encinas Dardengo et al. 2018). Further, polycultures of even a few species in other commercially important tropical tree species such as coffee have been shown to have higher stem density (López-Gómez et al. 2008) and in some cases higher total production (Power and Flecker 1996). Thus, these polycultures may also be more efficient for production than their monoculture counterparts despite their lower yield of *T. cacao* (Haggar and Ewel 1997, Erskine et al. 2006). A meta-analysis of tropical tree plantations found that mixtures had higher growth rates than monocultures across economically important tree species (Piotto 2008). These increases in primary production are often also closely linked to increased carbon sequestration in tropical plantations (Brown et al. 1986; Saj et al. 2017).

Further, planting agriculturally important tropical tree species in polyculture rather than monoculture may allow them to better provide habitat for other species. The tree species we studied produced flowers and buds, and their flowers were open at similar times, suggesting that they may share pollinators. If these species share pollinators, then polyculture may support pollination efficiency and increase the recruitment of pollinators due to increased floral abundance (Chen and Hsu 2011). However, in spite of the similarities in flowering and our small sample sizes, these species had significantly different timing in their pod production (Fig. 5). The differences in pod production may indicate that these species share dispersers and vary their pod production so as not to compete for dispersers. Alternatively, differences in pod production may indicate that these species have different seed dispersal agents. In either case, polyculture will likely support either a single dispersal agent if species share dispersers or the diversity of dispersal agents if species do not share dispersal agents by providing seeds at different times in the year.

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