Phenological strategies of *Annona* species from the tropical deciduous forest of Chiapas, Mexico

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Abstract

Background. Phenological descriptions of plant species are used to understand cycles of foliation, flowering and fruiting. These studies provide useful means for understanding the relationships between plants and their environment.
Question. What are the the foliar and reproductive strategies of four species of *Annona* living in the Deciduous Forest of Chiapas, Mexico?
Species studied. *Annona lutescens*, *A. macroprophyllata*, *A. reticulata* and *A. purpurea*.
Study sites. Three areas of deciduous forest were studied (16°31’36’’ N, 92°58’25’’ W, 16°28’82’’ N, 92°57’48’’ W, and 16°21’47’’ N, 92°58’32’’ W), located between the towns of Parral and Chiapa de Corzo, Chiapas, Mexico.
Method. Stages of foliation, flowering, fruiting and senescence of 20 individuals per species were documented by written and photographic records during the course of a year. Variable time periods were adapted to the extended BBCH scale. The phenology was correlated with the stages of rain and drought by Spearman’s correlations
Results. Phenological characteristics distinguish *A. reticulata* and *A. lutescens* as species with a reproductive strategy (flowering and fruiting) synchronized with the dry months, in contrast to *A. purpurea* and *A. macroprophyllata*, which show a reproductive strategy associated with the rainy season. The foliation of the four species is phenologically related to the rainy season.
Conclusions. The species studied could be grouped according to their leaf pattern as brevideciduous or deciduous and according to their reproductive pattern as having long-term or short-term strategies.
Keywords: Annonaceae, BBCH, foliation, flowering, fruiting

Estrategias fenológicas de especies de *Annona* en una selva baja caducifolia de Chiapas, México

Resumen

Antecedentes. Las descripciones fenológicas de las especies vegetales son usadas para conocer los ciclos de foliación, floración y fructificación de las plantas cultivadas, estos estudios proveen herramientas útiles para comprender las relaciones entre las plantas y su ambiente.
Preguntas. ¿Cuáles serían las estrategias foliares y reproductivas de cuatro especies del género *Annona* que habitan en la Selva Baja Caducifolia de Chiapas, México?
Especies en estudio. *Annona lutescens*, *A. macroprophyllata*, *A. reticulata* y *A. purpurea*
Sitio de estudio. Se estudiaron tres áreas de la selva baja caducifolia, localizada entre los municipios de Chiapas de Corzo y Parral, en Chiapas, México (16° 31’ 36’’ N, 92° 58’ 25’’ W; 16° 28’ 82’ ‘N, 92° 57’ 48’’ W, and 16° 21’ 47’’ N, 92° 58’ 32’’ W).
Métodos. Las etapas de foliación, floración, fructificación y senescencia de 20 individuos por especie se documentaron mediante registros fotográficos y escritos durante un año y en periodos de tiempo variable y se adecuaron a la escala BBCH extendida. La fenología y las etapas de lluvia y sequía se asociaron a través de correlaciones de Spearman.
Resultados. Las características fenológicas distinguen a *A. reticulata* y *A. lutescens* como especies con estrategia de reproducción (floración y fructificación) sincronizadas con los meses de secas, contrastando con las de *A. purpurea* y *A. macroprophyllata* que están asociadas a la época de lluvias. La fenología de foliación de las cuatro especies está relacionada con la época de lluvias.
Conclusiones. Las especies estudiadas pudieran agruparse de acuerdo a su patrón foliar en brevideciduas y deciduas y de acuerdo a su patrón reproductivo en especies con estrategias largas y cortas
Palabras clave: Annonaceae, BBCH, foliación, floración, fructificación

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Tropical dry forests (TDFs) account for over 42 % of the world's tropical forests (Murphy & Lugo 1986), and the floristic region of the "Central Chiapas Depression" in Mexico is among the most diverse (Olson *et al*. 2001, Sousa 2010). One characteristic of this floristic region is the alternation of the rainy and dry seasons, which conditions plants to follow characteristic phenological patterns, including the length or the interactions of leaf development and the flowering and fruiting periods. In such environments, most species are deciduous, with leaf drop occurring at the beginning of the dry season and foliation after the first rains. The most common patterns include flowering in the rainy season (Bullock & Solís-Magallanes 1990); in other cases, the beginning of the reproductive stage occurs during the dry period (Singh & Kushwaha 2006). However, certain species show less common patterns, such as those with evergreen habits (Choat *et al*. 2005, Rojas-Jiménez 2007), including some *Cordia* species in Mexico and Central America. For example, *Cordia alliodora* has been classified as a wet-season deciduous tree (Choat *et al*. 2007).

Various leaf phenological patterns are observed in TDFs, and according to Borchert *et al*. (2002), these patterns are related to the distribution of precipitation throughout the year. Rivera & Borchert (2001) and Singh & Kushwaha (2005) have described multiple foliar strategies, which are classified as deciduous, brevideciduous, evergreen and leaf exchange.

Brevideciduous species only lose their leaves during a short period in the dry season, and most of them have similar strategies to respond to drought (*Guazuma ulmifolia* and *Tecoma stans*). Almost all of them possess a water-use mechanism, such as increasing stem water potential, to obtain more water, and they increase their root mass to perform these processes. In contrast, deciduous trees begin senescence and the consequent caducity early in the dry season; they respond to drought with water-saving strategies, such as closing stomata, decreasing photosynthetic activity, minimizing stem water potential to save water in the roots and stem, and loss of foliage, which occurs in some species of *Tabebuia* (Chaves *et al*. 2003, Singh & Kushwaha 2005, Elliot *et al*. 2006). In evergreen species (*Couepia polyandra*, *Randia armata* and *Thouinidium decandrum*), foliar bud break begins weeks before all the old leaves have abscised. In TDF cohabite species, in which senescence and the production of new leaves is almost simultaneous, they retain a portion of their foliage throughout the year (evergreen) (Huante *et al*., 2002, Rivera *et al*. 2002). These environments also contain species with foliar replacement strategies, including *Pithecellobium saman*, *Simarouba glauca* and *Swietenia macrophylla* (Borchert *et al*. 2002, Rivera *et al*. 2002)

Trees in TDFs display several phenological patterns caused by seasonal variations in rainfall, changes in temperature and solar radiation (Nanda *et al*. 2014). There are species that flower and fructify when foliar senescence and caducity occur during the dry season, but other species flower and fructify during the rainy season. Winter reproduction is frequently found in certain species, and it can be related to environmental factors, such as photoperiod (Borchert *et al*. 2004) or the presence of pollinators, as well as the dispersal syndrome of each species.

The TDF is an ecosystem with a high diversity of plant species that are useful to humans, including plants that serve as food or medicine such as *Byrsonima crassifolia*, *Gliricidia sepium*, and *Guazuma ulmifolia* (Miranda 2015). The TDF of the Central Chiapas Depression contains wild trees of the Annonaceae family with food potential, such as *Annona lutescens* Saff. (anona amarilla), *A. macroprophyllata* Donn. Sm. (papausa), *A. reticulata* L. (anona roja), and *A. purpurea* Moc. & Sessé ex Dunal (chincuya). Some of these species are also found in home gardens and within live fences (González-Esquinca 2001).

These *Annona* species grow in the same area, but they have different reproductive habits; in particular, they disperse their seeds at different times of the year. Direct observations over several years show that *A. lutescens* and *A. reticulata* bear fruit at the end of the dry season, whereas *A. macroprophyllata* and *A. purpurea* do so at the end of the rainy season and the beginning of the dry season. The contribution of these four TDF trees to forest functioning is poorly understood (Castro-Moreno *et al*. 2013). In this paper, we describe and classify the phenological and morphological changes associated with their seasonal cycle for the first time. This information will contribute to our understanding of the life cycles of these tree species and their ability to respond to seasonal changes.

Materials and methods

Study area. The study area is located between the municipalities of Chiapa de Corzo and Parral in Chiapas State, Mexico. The studied tree species were found growing in three disturbed areas of TDF (16°31'36'' N, 92°58'25'' W; 16°28'82'' N, 92°57'48'' W, and 16°21'47'' N, 92°58'32'' W). The climate in the region is warm and subhumid, with summer rains (AW_1) and two seasons that are characterized as a dry season (October-May) and a rainy season (June-October). The average annual temperature is 25.8 °C, although maximum temperatures can reach 38 °C in exceptionally warm years, and the average annual rainfall is 921.9 mm (García 1988).

The climate of the study area was characterized using the precipitation and temperature data from Rivera de Zaragoza (municipality of Chiapa de Corzo) during 2013. The drought season corresponded to the months of November to April, when rainfall was below 46 mm, and maximum temperatures reached 26 °C. The rainy season occurred from June to September, with rainfalls of up to 265 mm and temperatures under 25 °C.

Phenological characterization. Considering that the studied tree species grow in disturbed areas, they were found in low densities. To perform this study, we selected 20 adult trees per species growing within the same area (approximately 5,000 m^2) to avoid possible variations due to environmental conditions. The plants were identified and numbered, and they were observed during the third week of each month. During the flowering stages, trees were recorded each day from December 2012 until February 2014 and documented photographically. The vegetative and reproductive stages were characterized using the modified, extended "Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie" (BBCH) scale described by Hess *et al*. (1997). Although this scale is used for cultivated plants, we elected to use it because the studied *Annona* species are potentially cultivable. The scale proposed by Hess *et al*. (1997) considers a 2-digit code, where the cycle of plant development is divided into ten clearly recognizable and distinguishable phases referred to as principal growth stages and numbered from 0 to 9 (first number). The secondary growth stages (second number) are used to more accurately identify the progression in growth during each principal growth stage. The following principal growth stages were used in our study: bud development (BBCH 0), leaf development (BBCH 1), flower growth (BBCH 5), full flowering (BBCH 6), fruit growth (BBCH 7), fruiting (BBCH 8), and senescence (BBCH 9). The second number includes clearly recognizable external features (Ta-

Table 1. Foliar phenology in *Annona* species. BBCH 0, 1 and 9.

Code	Description	*A. lutescens*	*A. macroprophyllata*	*A. purpurea*	*A. reticulata*
0	**Bud development**	June-April	June-April	June-April	June-April
00	Latent bud closed and covered	June-April	June-April	June-April	June-April
03	Foliar bud swollen	April	May	May	April
07	Beginning of bud breaking	April	May	May	April
09	Buds shows green or brown tips	April	May	May	April
1	**Leaf flushing and leaf display**	May-December	May-November	May-October	April-December
10	Leaves emerging Brownish scales slightly opened: leaf flushing	April-May	May-June	May-June	April-May
11	Branches with first leaves unfolded	May (light green color)	June (purplish red color)	June (purplish red color)	May (light green color)
15-18	50-80% of leaves unfolded	June	June	June	June
19	Unfolded leaves	June-December	July-November	July-October	June-December
9	**Senescense**	December-April	November - May	October - May	December-April
90	Mature leaves with some signs of senesce	December	December	November	December
93	The leaves change color (green to yellow)	December	December	November	December
95	50% of foliage loss	February	February	February	February
97	70-90% of leaf caducity	February	March	February	March
99	Foliage almost entirely loss	April	March-April	March-April	April

Table 2. Reproductive phenology of *Annona* species. BBCH 5 to 8.

Code	Description	*A. lutescens*	*A. macroprophyllata*	*A. purpurea*	*A. reticulata*
5	**Flower growth**	Nov-Dec	May-June	May-June	Nov-Dec
50	Flower buds are visible and closed	November	May	May	November
52	Flowers at final size	November	May	May	November
59	Flower still closed, with the final size	November	May	May	November
6	**Flowering**	December	May-June	May-June	December
60	The flower begin opening in pre-female state	2-3 days after stage 59 (24-48 hours of duration)	2-3 days after stage 59 (24-48 hours of duration)	2-3 days after stage 59 (24-48 hours of duration)	2-3 days after stage 59 (24-48 hours of duration)
61	Flower opening in the female state	24 hours	24 hours	24 hours	24 hours
65	Flower in male state, showing the stamens	12-24 h after the female stage	12-24 h after the female stage	12-24 h after the female stage	12-24 h after the female stage
68	The petals color begin to change from green to brown, and them can fall	24-36 hours	24-36 hours	24-36 hours	24-36 hours
7	**Development of fruit**	December-February	June-August	July-September	December-February
70	Gynoecium is a little swollen	December	June	July	December
71	Fruit set beginning of ovary swelling, light green color	December	June	July	December
79	Fruit in the final size	February	August	September	February
8	**Fruiting**	March- May	September-October	October-November	March- May
81	The green color change only in a little part in yellow color	12 days after attaining the final size	12 days after attaining the final size	12 days after attaining the final size	12 days after attaining the final size
89	End of fruiting, fruits fall	May	September-October	October-November	May

bles 1-2) corresponding to the secondary stages of plant development. The herbarium samples were checked against the specimens deposited in the Herbarium Eizi Matuda (HEM) of the Universidad de Ciencias y Artes de Chiapas (UNICACH) using the following record numbers: *A. lutescens* (ARGE 352), *A. macroprophyllata* (ARGE 345), *A. purpurea* (ARGE 348), and *A. reticulata* (47155). To classify flowering and fruiting stages, the Newstrom *et al*. (1994) classification was used.

To determine the association between climatic factors (rainfall, monthly total and maximum, minimum and average temperature) and the phenology of the species, Spearman's correlations were performed. For this purpose, data were grouped into reproductive stages (flowering and fruiting) and growth phases (leaf development and senescence).

Results

Foliar phenology. In all species, visibility of dormant buds was higher when the trees lost their leaves (BBCH 00); leaf bud development in *Annona lutescens* and *A. reticulata* began at the end of the dry season, while that of *A. macroprophyllata* and *A. purpurea* began during the transition from the dry season to the rainy season (BBCH 03) (Table 1). The branches produced mixed buds (vegetative and floral), and in all of the species, they were both terminal and axillary.

The leaf buds of *Annona lutescens*, *A. macroprophyllata*, and *A. reticulata* were usually coated with whitish laminar cataphylls (BBCH 03) that broke when the leaves emerged (Figure 1H). In contrast, *A. purpurea* buds were covered by two or more pubescent cataphylls (BBCH 03) that resembled a cap when the buds opened (BBCH 07, Figure 1L) and eventually showed the first green or brown buds (BBCH 09). In all of the species, the first leaves emerging from the buds were initially covered in abundant golden-brown hairs.

Leaf development. Leaf flushing (branches with first leaves unfolded) in these trees began in May after the dry season and sometimes occurred before the rains, and the leaves emerged from the leaf buds after three to four days (BBCH 11). The leaf buds of *Annona macroprophyllata*

Figure 1. Some development state of *Annona* species. **A-D**, *Annona lutescens*. A, Flowers in distinct development state. B, Male flower. C, Fruit. D, Flower bud. **E-H**, *Annona macroprophyllata*. E, Female and male flowers. F, male flower. G, Developing fruit. H, Leaf bud. **I-L**, *Annona purpurea*. I, Flower female. J, the flower is used as chamber pollination by Coleoptera. K, Developing fruit. L, Leaves buds. **M-P**, *Annona reticulata*. M, Male flower. N, Female flower. O, Fruit. P, Branch with leaves and flower fertilized

were the only ones that produced an initial pair of nonpetiolate leaves, which were orbicular with brown hairs on the cataphylls and the margins. The presence of this type of leaf indicated the development of branches simultaneously bearing leaf buds and flowers, but the remaining branches, formed from apical buds, lacked floral buds. Twenty days after the rains began, the branches of the four species exhibited leaves in various stages of development, with the youngest leaves located apically (BBCH 12-19). When the rains ended, most of the trees displayed abundant foliage and fully developed branches (BBCH 19, BBCH 39).

Leaf senescence. At the onset of the drought season, the young plants started to show leaf senescence, and leaf senescence was detected later on the mature trees. Leaf senescence was characterized by the loss of leaf turgor, a gradual chlorosis up to the time of leaf fall, and the beginning

Table 3. Reproductive strategies of *Annona* species from deciduous lowland forest

Phenological phase	Early drought reproductive strategy (EDRS) *Annona lutescens* & *Annona reticulata*	Late drought reproductive strategy (LDRS) *Annona macroprophyllata* & *Annona purpurea*
Flowering	Beginning of the dry season	End the dry season and during all rainy season
Fruiting	During the dry season	During the rainy season
Germination	Seed without dormancy, immediate germination	Seed with dormancy, seeds do not germinate until the beginning of the next wet season

of latency in the leaf buds. The end of vegetative activity occurred during this period, and no new leaves were formed (BBCH 91). At the beginning of the dry season, there were trees with symptoms of leaf senescence, and in all of the species, the leaves turned from green to yellow and then to brown (BBCH 93). The trees lost more than 50 % of their leaves (BBCH 95) during February, and by early March, they only retained 10 % of their senescent leaves (BBCH 97). Finally, during the last weeks of March and April, the trees became leafless (BBCH 99). The behaviour of the four species was similar, although *Annona lutescens* and *A. reticulata* usually retained some proportion of their foliage; these species appeared more drought resistant than the other two *Annona* species.

Reproductive phenology. *Annona lutescens* and *A. reticulata* flowered sporadically throughout the year, but most of the flowers were aborted. Full flowering occurred only during November and December (Table 2). The flowers that emerged at the beginning of the dry season were the only ones that produced fruit. The flowering of *A. macroprophyllata* and *A. purpurea* only occurred in May and June. *Annona lutescens* and *A. reticulata* fruited at the end of the drought season, but the other two species produced fruit during the middle and at the end of the rainy season.

Emergence of flowers and flowering. In *Annona lutescens* and *A. reticulata*, the development of flowers usually lasted from one to two weeks. The flower buds were green, visible and located on branches with leaves (BBCH 50, Figure 1D). Each flower bud contained from one to six flowers at different stages of development: barely visible, one-fourth of their final size (BBCH 52, Figure 1A, M), one-half of their final size (BBCH 55), and closed flowers at their final size (BBCH 59). The inflorescences were opposite to the leaves or implanted at the mid-part of an internode and were composed of several individual pedicellate flowers with very small triangular sepals and three greenish-yellow outer petals. In *A. macroprophyllata*, the leaves and flowers developed simultaneously, and the flowers were single and possessed a pedicel (Figure 1E-F). However, the flowers of *A. purpurea* were single or arranged in pairs (Figure 1I) and were subsessile and extra-axillary.

The flowers of all species exhibited dichogamy. They had a prefemale state (BBCH 60) when the petals were closed or slightly opened, and this stage lasted for 24 to 48 hrs. In the female state (BBCH 61, Figure 1E, N), the petals were partially opened, the stigma was visible and bright, and the release of scent was perceptible; the pollination period lasted up to three days. The male state (BBCH 65, Figure 1B, F, M) was observed when the petals were completely open and the visible stamens were separated, releasing the pollen. *Annona macroprophyllata*

Table 4. Spearman correlation (and it *p* value) between reproductive phenology and climatic variables for the species of *Annona*

	Monthly Precipitation	Maximum Temperature	Minimum Temperature	Average Temperature
A. lutescens	-0.83 (0.0001)	-0.28 (0.23)	-0.80 (0.0001)	-0.36 (0.13)
A. macroprophyllata	0.78 (0.0001)	0.35 (0.15)	0.89 (0.0001)	0.39 (0.09)
A. purpurea	0.63 (0.004)	0.21 (0.39)	0.63 (0.003)	0.27 (0.27)
A. reticulata	-0.59 (0.007)	0.17 (0.47)	-0.68 (0.0001)	0.095 (0.69)

Table 5. Spearman correlation (and it *p* value) between vegetative phenology and climatic variables for the species of *Annona*

	Monthly Precipitation	Maximum Temperature	Minimum Temperature	Average Temperature
A. lutescens	0.60 (0.006)	-0.02 (0.93)	0.60 (0.006)	0.03 (0.90)
A. macroprophyllata	0.70 (0.0008)	0.14 (0.56)	0.75 (0.0002)	0.20 (0.41)
A. purpurea	0.78 (0.0001)	0.29 (0.21)	0.92 (0.0001)	0.35 (0.14)
A. reticulata	0.61 (0.006)	0.0001 (0.99)	0.60 (0.006)	0.03 (0.90)

possessed red-brown pubescent petals, which were usually retained for several days (BBCH 68, Figure 1G), and a purple androecium that was distinguishable from the cream-coloured gynoecium. In *A. lutescens* and *A. reticulata*, the petals were yellowish-green, while *A. reticulata* was distinguished by red coloration at the base of the inner and the outer walls of the petals (Figure 1N). In both cases, the petals turned brown and fell off at the end of flowering. The petals of *A. purpurea* appeared velvety with purple on the inside and creamy yellow on the outside and dropped slightly earlier than the petals of the other species. This process may have been due to the numerous beetles that used the floral cavity for copulation (Figure 1J).

Growth of fruit and fruiting. With fruit development, the petals fell in all of the species with the exception of *Annona macroprophyllata*, whose petals tended to be more persistent (BBCH 70, Figure 1G). After this stage, the fruit that had not set fell off the plant, while those that had set grew (BBCH 71); fruit at various stages of development was visible on the same tree (Figure 1G, K). The fruit reached one-half of its final size and full size at approximately 70 days (BBCH 75) and 120 days (BBCH 79) after pollination, respectively. All of the species were found to have climacteric fruit (Table 2).

On all of the trees, it was possible to find fruit in the following stages of development: (1) fruit with incipient maturity that changed from green to yellow (*Annona lutescens*) or from green-purple to red (*A. reticulata*) (Figure 1C, O), with the fruit of *A. macroprophyllata* and *A. purpurea* remaining green or slightly brown (BBCH 81); (2) fruit with firm flesh mature enough for harvest (BBCH 87); and (3) fruit mature enough for consumption, with an intense aroma and colour and a smooth texture (BBCH 89). The fruit ripened quickly, so they could not be stored for more than four to seven days; in particular, the fruit of *A. macroprophyllata* broke open while still on the tree, showing a white or pink-coloured pulp.

The correlation analysis between climatic factors and phenology of *Annona* species shows that the reproductive phases of species are associated with changes in precipitation and minimum temperatures; these environmental factors also bind *A. macroprophyllata* and *A. purpurea*, as species requiring the presence of rain with decreasing temperature for fructification, whereas *A. lutescens* and *A. reticulata* do not require these conditions to bear fruit (Table 4). In contrast, the strategy of foliation is similar among the four species and is triggered by the start of precipitation and the consequent decrease in temperature (Table 5).

Discussion

In TDFs, many plant species may respond to the same climatic conditions in contrasting ways through different physiological, phenological, and morphological adaptations. In particular, our study shows that *Annona* species in the Central Chiapas Depression show different vegetative and reproductive phenological patterns (Tables 1 and 2). Our results also show that *A. lutescens* and *A. reticulata* could be brevideciduous species (Singh & Kushwaha 2005) because their foliar caducity period (three months) is shorter than that of *A. macroprophyllata* and *A. purpurea*, which are deciduous species (six months) (Figure 2).

The flowering of these species is annual and intermediate (Newstrom *et al*. 1994), with a duration of about two months, but trees of *Annona lutescens* and *A. reticulata* with flowers out of season can be observed.

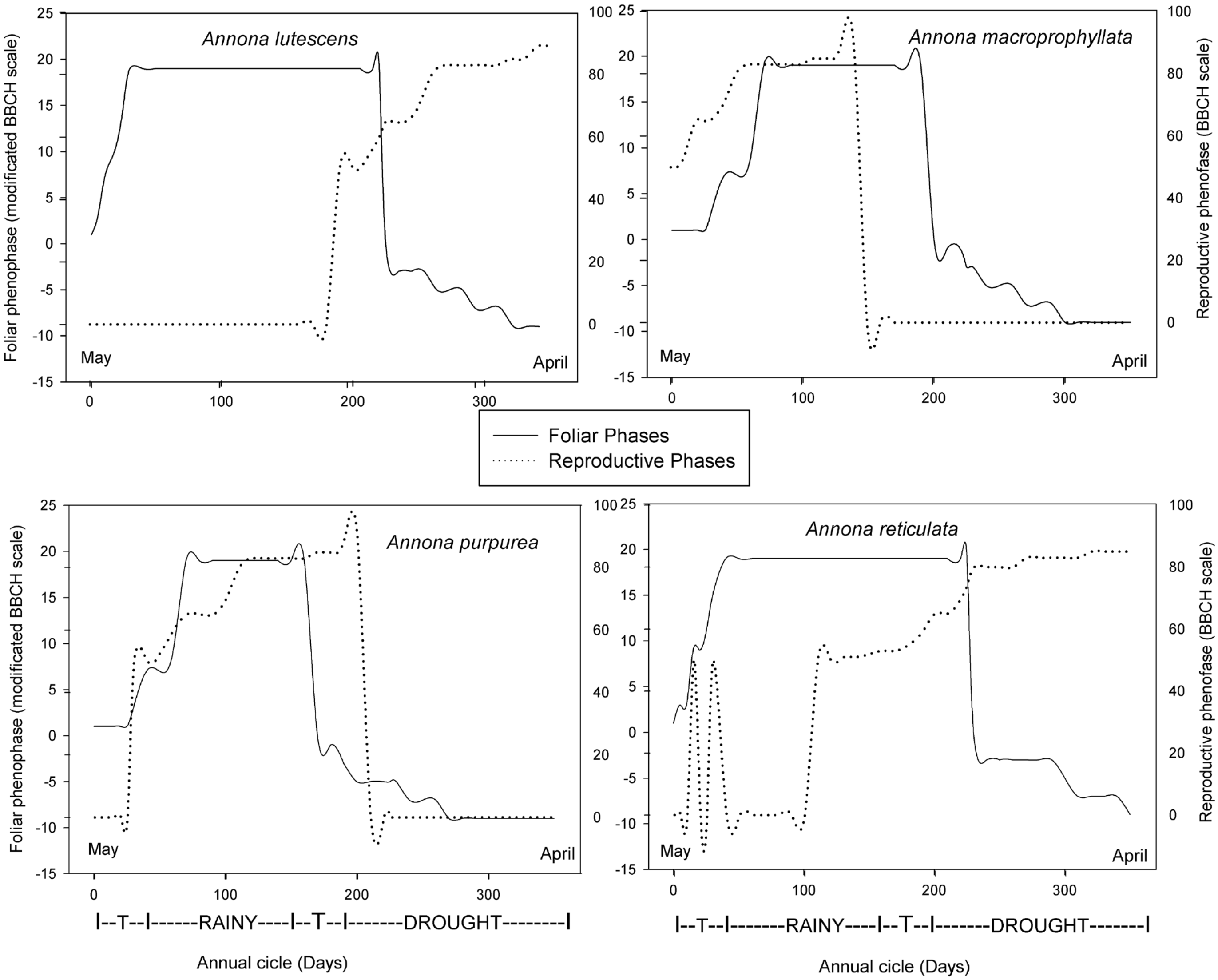


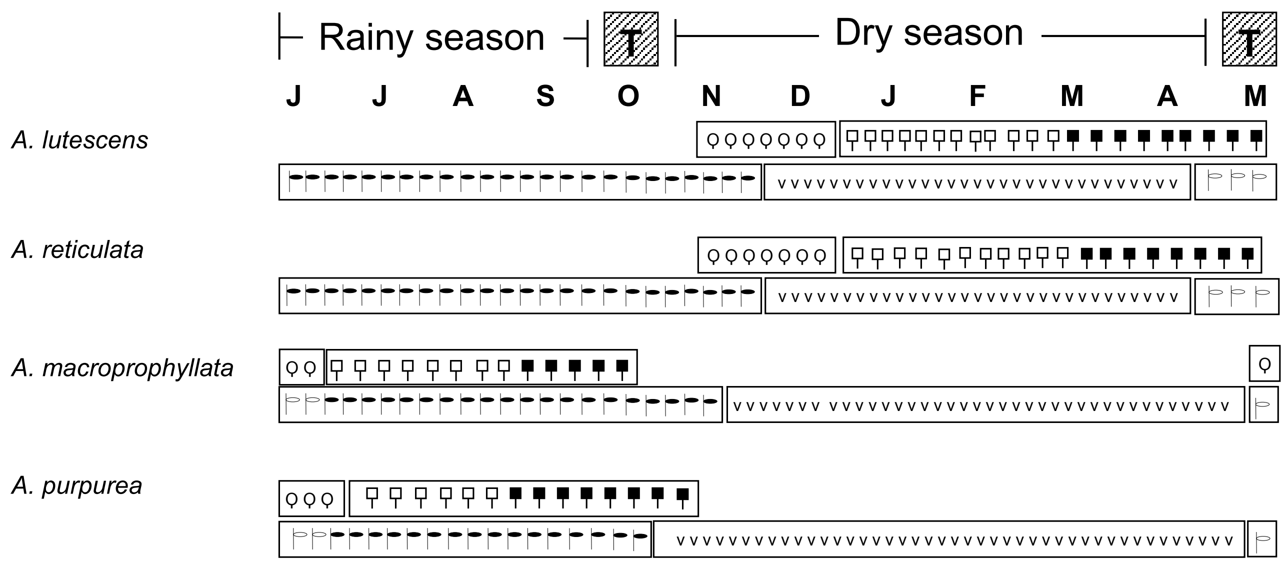
Figure 2. Foliar and reproductive phases adjusted of BBCH scale.

Annona lutescens and *A. reticulata* start flowering at the beginning of the dry season and begin fruiting at the end of the dry season (Figure 2), and their seeds can germinate immediately after fruiting. However, *A. macroprophyllata* and *A. purpurea* had flowers at the end of the dry season and towards the beginning of the rainy season and began fruiting at the end of the rains. Their seeds likely remain dormant for at least six months or until the next rainy season starts (González-Esquinca *et al*. 2014).

These features suggest that the two groups of species have different climatic requirements (Tables 4 and 5) and that seed dormancy in *Annona macroprophyllata* and *A. purpurea* provides an escape from the extreme conditions found in the TDF during the dry season, increasing the probability of seedling survival during the following rainy season (Figure 3).

The reproductive responses of *Annona lutescens* and *A. reticulata* showed a negative Spearman correlation with rainy period, whereas *A. macroprophyllata* and *A. purpurea* showed positive Spearman correlations with the rainy period; these features allow us to suggest their categorization in early dry reproductive strategy (EDRS) and late dry reproductive strategy (LDRS) groups, respectively (Table 3). Note that phenological data for *A. lutescens* (Castro-Moreno *et al*. 2013) from another TDF area corroborate our classification of the species.

This study indicates that foliage display occurs during the rainy season in the four *Annona*



		J	J	A	S	O	N	D	J	F	M	A	M
Precipitation mm	Maximum	51.7	20.4	40.4	106	24.7	1.8	1.7	0.1	0	0.1	24.5	48.4
	Minimum	0	0	0	0	0	0	0	0	0	0	0	0
	Monthly	**213**	**71.6**	**165**	**265**	**41.2**	**9.5**	**1.8**	**0.1**	**0**	**0.2**	**45.8**	**91.4**
Temperature °C	Maximum	26.9	26.3	26.5	26.3	30.3	25.6	23.7	25.6	26.1	29.8	31.5	33.2
	Minimum	22.5	22.8	23.5	21.7	23.2	18.7	19.6	18.1	20.3	18.8	19.9	21
	Mean	**24.8**	**24.3**	**24.6**	**24.3**	**26.9**	**22.8**	**22**	**22.4**	**24.3**	**24.8**	**26.2**	**27.6**

Phenophase: Flowering, Immature Fruit, Mature Fruit, Leaf flushing, Foliage display, v Senescence, T Transition

Figure 3. Phenology of *Annona* species during an annual cycle.

species, which are typically deciduous species (Figure 3), but that leaf duration varies. *Annona lutescens* and *A. reticulata*, the EDRS species, were observed to tolerate drought longer than the other two species before reaching leaf senescence and expiration, i.e., they are the more desiccation-tolerant species. Shorter foliage displays were found in *A. macroprophyllata* and *A. purpurea*, the LDRS species. The results indicated that the leaves of *A. lutescens* and *A. reticulata* begin to senesce after three months of drought, and the trees only become almost leafless in the final dry months (brevideciduous). Additionally, leaf flushing begins days before the start of the rains. Perhaps the large density of lenticels on the stems of the EDRS species allows them to survive in drought (Figure 1D, H); in fact, desiccation tolerance has been reported in *A. lutescens* (Castro-Moreno *et al*. 2013), the most likely of the four *Annona* trees to have the highest drought resistance. Rivera *et al*. (2002) discussed the importance of increased photoperiod in certain species for initiating foliation before the rains, and these plants may also perceive increases in relative humidity or temperature prior to the establishment of the rainy season.

The above characteristics distinguish *Annona lutescens* and *A. reticulata* as species whose reproduction and survival strategies are synchronized with the climatic conditions of the TDF. By contrast, the characteristics of *A. purpurea* and *A. macroprophyllata* indicate lesser resistance to drought, which may explain their presence in ecotones of tropical sub-dry forest (Tables 4 and 5).

The phenology of *Annona* species has been previously described only for two cultivated species, cherimoya (*A. cherimola*, Cautin & Augusti, 2005) and the floral stages of soursop (*A. muricata*, Yamarte *et al*., 2004), and for a single wild species (*A. lutescens*, Castro-Moreno *et al*. 2013). An understanding of the vegetative and reproductive patterns of wild species and their relationships with the animals that depend on them (e.g., herbivores, pollinators, and fruit bats; Figure 1J) allows us to comprehend the response of plants to the climatic conditions of a particular area and facilitates the use of sustainable production and harvest strategies for wild edible species with the potential for cultivation, like those described in this study. Phenological characterizations also allow the establishment of study models to determine and predict the physiological and morphological responses that plants have developed to the changing environment over evolutionary history.

Further studies of the ecophysiology and morphology of these trees can potentially determine whether any of these adaptations may confer resistance to climate change, allowing the trees to serve as an alternative crop for reforestation.

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