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POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD

ECOLOGÍA

EFECTOS DE LA HERBIVORÍA Y TEMPORALIDAD EN EL ÉXITO REPRODUCTIVO DE *Casearia nitida* Jacq. (L) (Salicaceae)

TESIS

(**POR ARTÍCULO CIENTÍFICO**)

EFFECTS OF HERBIVORY AND ITS TIMING ON A TROPICAL DECIDUOUS TREE REPRODUCTIVE SUCCESS

QUE PARA OPTAR POR EL GRADO DE:

MAESTRA EN CIENCIAS BIOLÓGICAS

PRESENTA:

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MORELIA MICHOACÁN, SEPTIEMBRE, 2020

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P r e s e n t e

Me permito informar a usted que en la reunión ordinaria del Subcomité de Ecología y Manejo Integral De Ecosistemas del Posgrado en Ciencias Biológicas, celebrada el día **24 de febrero de 2020** se aprobó el siguiente jurado para el examen de grado de **MAESTRA EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **Ecología** de la alumna **QUIROZ PACHECO ENYA NICOLE**, con número de cuenta **380218525** por la modalidad de graduación de **tesis por artículo científico** titulado: **"Effects of herbivory and its timing on a tropical deciduous tree reproductive success",** que es producto del proyecto realizado en la maestría que lleva por título: "**Efectos de la herbivoría y temporalidad en el éxito reproductivo de *Casearia nítida* Jacq.(L)(Salicaceae)",** ambos realizados bajo la dirección de la **DRA. EK DEL VAL DE GORTARI,** quedando integrado de la siguiente manera:

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Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARÁ EL ESPÍRITU"
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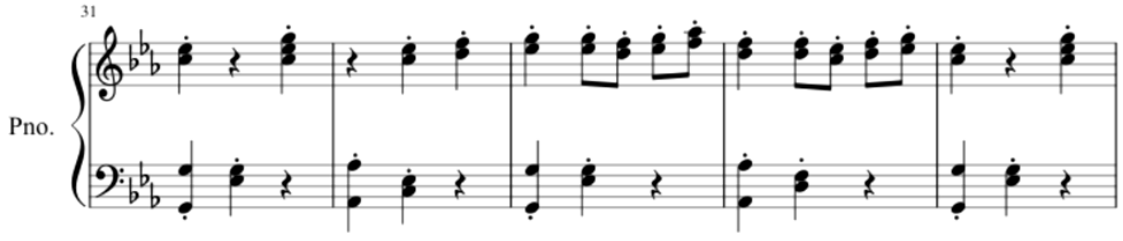

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RESUMEN

Las repercusiones de la herbivoría sobre la reproducción vegetal se han estudiado ampliamente, no obstante, es complejo determinar los alcances de la defoliación sobre el éxito reproductivo, ya que hay una enorme cantidad de factores que interactúan entre sí, modificando los efectos que tienen. En el presente estudio se busca mostrar cómo impacta el daño foliar a través del tiempo sobre varios caracteres reproductivos, tanto femeninos como masculinos; y cómo se relacionan éstos elementos (tanto daño foliar como caracteres reproductivos) entre sí. Así mismo, se investigó si hay algún momento en el que la herbivoría tiene mayores repercusiones sobre el éxito reproductivo de la planta. Para ello se evaluó el impacto de la herbivoría foliar en tres momentos fenológicos, sobre el éxito reproductivo de *Casearia nitida* (L.) Jacq. (Salicaceae). Se realizaron censos florales, conteos de frutos, colecta de hojas, de flores y de frutos, durante dos temporadas consecutivas en 48 plantas de *C. nitida*. El daño foliar tuvo un impacto diferencial sobre los caracteres reproductivos evaluados, de acuerdo al estado fenológico temporal de los individuos. El daño acumulado tuvo un mayor impacto negativo sobre el número de inflorescencias, flores, número de granos de polen, y de manera indirecta en el número de infrutescencias y frutos, así mismo tuvo una relación positiva con la herbivoría foliar durante la floración. Este estudio permite visualizar efectos en cascada del daño foliar en diferentes estados fenológicos mediante las relaciones internas de los caracteres.

ABSTRACT

The repercussions of herbivory on plant reproduction have been widely studied, however, it is complex to determine the scope of defoliation on reproductive success, because there is a huge quantity of interacting factors that modify the responses we see. In this study it is intended to show how foliar herbivory changes trough time impact several reproductive characters, both male and female, and how these elements are affected among themselves (both herbivore damage and reproductive characters). Likewise know if there is any time when herbivory has a bigger impact in terms of reproductive success. For this the impact of foliar herbivory on reproductive success was evaluated in three different phenological moments of *Casearia nitida* (L.) Jaqc, (Salicaceae). Floral censuses, fruit counts and collection of leaves, flowers and fruits were made for two consecutive seasons on 48 plants of *C. nitida*. Foliar herbivory had a differential impact on reproductive characters depending on the individual's phenological state. The accumulated damage had a bigger impact, with negative effects on the number of inflorescences, flowers and pollen grains, indirectly affected the number of infructescences and fruits, also increased foliar damage during flowering. This study allows visualizing cascade effects through time and internal relationships of reproductive traits with herbivore damage.

INTRODUCCIÓN

Las plantas se encuentran expuestas de manera constante a patógenos y herbívoros, por lo que evolutivamente han desarrollado mecanismos que les permiten sobrevivir y dejar descendencia, aún en presencia de agentes dañinos. Comúnmente las plantas poseen más de una característica de defensa y pueden alternar entre una y otra, dependiendo del estado ontogenético, tipo de daño, recursos disponibles y temporada (Gong and Zhang 2014). De manera general se pueden distinguir tres formas principales de lidiar con la herbivoría: resistencia, tolerancia y escape (Boege *et al.* 2011; del-Val 2012). El primer caso se refiere a las defensas químicas, físicas y bióticas (Gong and Zhang 2014), en el segundo a la capacidad de reducir los efectos negativos del daño en la adecuación del individuo, como es el caso de la compensación (Fornoni 2011). Finalmente el escape implica reducir la probabilidad de ser encontradas por el herbívoro o patógeno, mediante cambios fenológicos, asociaciones con otras especies, etc. (Gong and Zhang 2014).

Más allá de la o las estrategias que utiliza cada planta, la herbivoría implica una pérdida de tejido, y en el caso de las hojas una reducción del área fotosintética, así como una movilización de recursos producidos o almacenados (Koptur *et al.* 1996; Mutikainen and Delph 1996); como consecuencia, la herbivoría tiene un impacto en la dinámica interna de cada planta. La estrategia con que las plantas asignan recursos a las funciones vitales varía, dependiendo de la especie y condiciones ambientales (Bazzaz *et al.* 1987). No obstante, suele haber disyuntivas entre las diferentes funciones, por ejemplo entre tolerancia y defensa o entre crecimiento y defensa, entre muchas otras (Leimu and Koricheva 2006; Boege *et al.* 2007; Huot *et al.* 2014; Züst and Agrawal 2017).

Por otro lado, la reproducción si bien es un aspecto fundamental en el ciclo de vida de cualquier planta, implica una fuerte inversión de recursos (Noordwijk and Jong 1986). Incluso se ha visto que la reproducción en una temporada puede reducir la probabilidad de reproducirse a la siguiente, así como disminuir la probabilidad de sobrevivencia (Bazzaz *et al.* 1987). Hay quienes ven a la senescencia de la planta como un agotamiento de recursos. Por estas razones, las estrategias, con que los individuos asignan sus recursos a distintas funciones resulta fundamental en el ciclo de vida (Bazzaz *et al.* 1987).

La herbivoría puede tener efectos diferenciales en el éxito reproductivo y adecuación de las plantas. En general ocurre un efecto negativo (Dominguez and Dirzo 1994; Koptur *et al.* 1996;

Strauss and Irwin 2004; Boege 2005a), aunque hay algunos casos donde no se ha detectado tal efecto (Obeso and Grubb 1993; Strauss *et al.* 2001), incluso bajo ciertas condiciones puede llegar a ser positivo (Yamauchi and Yamamura 2004). En una amplia variedad de trabajos para medir el impacto de la herbivoría se toma en cuenta el número de flores, semillas y frutos, producidos bajo tasas de herbivoría foliar manipuladas. Sin embargo, la respuesta puede ser diferente bajo daño natural y artificial (Strauss 1988; Baldwin 1990), y se suele utilizar sólo la herbivoría pre o post floración, sin tomar en cuenta que la herbivoría puede fluctuar dentro y entre temporadas.

Adicionalmente el componente masculino y femenino en plantas, tanto dimórficas como monomórficas no siempre está correlacionado o se comporta de forma paralela (Mutikainen and Delph 1996), lo que puede promover una subestimación del éxito reproductivo, cuando se evalúan únicamente elementos del componente femenino (frutos y semillas). Incluso algunos individuos pueden tener un mayor éxito reproductivo vía masculina mientras que en otros es vía femenina (Quesada *et al.* 1995; Mutikainen and Delph 1996; Strauss *et al.* 1996). Del mismo modo, hay elementos periféricos que aunque estrictamente no forman parte de los verticilos sexuales y/o del aprovisionamiento de la semilla, son muy importantes. Se ha reportado, sobre todo en plantas que requieren de la entrecruza, que una alta proporción del esfuerzo reproductivo se asigna a tejidos periféricos destinados a la atracción de polinizadores y dispersores. Así los costos de la reproducción no se limitan únicamente a gametos y semillas (Wenk *et al.* 2017). Estos elementos periféricos, tales como el tamaño de la corola, cantidad de néctar, volátiles, entre otros, son afectados por la herbivoría foliar (Strauss *et al.* 1996; Strauss 1997; Suárez *et al.* 2009; Lucas-Barbosa *et al.* 2016). Aunque la relación éxito reproductivo-herbivoría es explícita, evaluar los verdaderos efectos globales de la herbivoría es difícil.

Los factores abióticos también influyen en el proceso reproductivo de las especies. Por ejemplo en el caso de la selva baja caducifolia, el agua tiene un papel fundamental (Bullock and Solis-Magallanes 1990; Cortés-flores *et al.* 2017), pues la estacionalidad es altamente marcada. Esta situación de estrés posiblemente incrementa la presión por herbivoría, ya que el crecimiento y reproducción ocurren en un período de tiempo limitado. Asimismo la actividad de los herbívoros se concentra en los pocos meses que abarca la temporada lluviosa (Dominguez and Dirzo 1994; Filip *et al.* 1995).

Las plantas leñosas de selva baja caducifolia han desarrollado una amplia variedad de estrategias que les permiten sobrevivir a la marcada estacionalidad (Reich and Borchert 1984; Reich 1995), el

más notorio es la pérdida de follaje durante la sequía; sin embargo, hay otros menos evidentes, como lo es la floración proléptica. En el primer caso, la senescencia del follaje implica muerte celular programada, un proceso complejo altamente regulado donde los elementos de un órgano pueden ser usados en otra estructura (Rentería *et al.* 2005; Taiz and Zeiger 2010; Rentería and Jaramillo 2011). En el segundo caso, la inducción a la floración ocurre al final de la temporada lluviosa. Posteriormente viene un periodo de latencia del meristemo promovido por la sequía, el cual es roto por la siguiente temporada lluviosa, disparando la floración de ese año (Borchert 1983). En este tipo de floración no está del todo esclarecido el mecanismo que marca el cambio de la fase vegetativa a la reproductiva, pero parece ser disparado por factores endógenos (Borchert 1983). No obstante, se ha propuesto que la senescencia del follaje juega un papel importante.

En este contexto, la cantidad de daño sufrido por una planta durante una temporada tiene efecto en los recursos que redistribuye durante la senescencia del follaje y lo que puede asignar al inicio de la siguiente. El efecto es aún más sensible en las especies prolépticas, ya que el daño foliar que ocurrió durante esa temporada, influirá en el número de meristemos en los que se puede dar el cambio de fase (vegetativa a reproductiva), reflejándose en las flores que se desarrollaran en la siguiente temporada. Por lo anterior, en el presente estudio se evaluó mediante el uso de análisis de ecuaciones estructurales, cómo afectan las fluctuaciones en el daño foliar a través del tiempo, a caracteres reproductivos tanto femeninos como masculinos. Así mismo se estimó si hay algún momento de la temporada en que la herbivoría tenga más repercusiones en términos de éxito reproductivo. El estudio pretende generar un panorama general, sobre cómo la adecuación e interacciones entre las variables endógenas (Inflorescencias, flores, crecimiento vegetativo, infrutescencias, frutos, semillas, diámetro floral, óvulos, tamaño y número de granos de polen) se ven afectados por la herbivoría en diferentes estados fenológicos de la especie proleptica *Casearia nitida*.

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Effects of herbivory and its timing on reproductive success of a tropical deciduous tree

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• **Background and Aims** The implications of herbivory for plant reproduction have been widely studied; however, the relationship of defoliation and reproductive success is not linear, as there are many interacting factors that may influence reproductive responses to herbivore damage. In this study we aimed to disentangle how the timing of foliar damage impacts both male and female components of fitness, and to assess when it has greater impacts on plant reproductive success.
• **Methods** We measured herbivore damage and its effects on floral production, male and female floral attributes as well as fruit yield in three different phenological phases of *Casearia nitida* (Salicaceae) over the course of two consecutive years. Then we tested two models of multiple causal links among herbivory and reproductive success using piecewise structural equation models.
• **Key Results** The effects of leaf damage differed between reproductive seasons and between male and female components of fitness. Moreover, the impact of herbivory extended beyond the year when it was exerted. The previous season's cumulated foliar damage had the largest impact on reproductive characters, in particular a negative effect on the numbers of inflorescences, flowers and pollen grains, indirectly affecting the numbers of infructescences and fruits, and a positive one on the amount of foliar damage during flowering.
• **Conclusions** For perennial and proleptic species, the dynamics of resource acquisition and allocation patterns for reproduction promote and extend the effects of herbivore damage to longer periods than a single reproductive event and growing season, through the interactions among different components of female and male fitness.

Key words: *Casearia nitida*, deciduous tree, female fitness, foliar damage, herbivory, male fitness, proleptic species, reproductive success, Salicaceae, structural equation model, tropical dry forest.

INTRODUCTION

Plants are continuously exposed to pathogens and herbivores throughout their lives, so they have evolved mechanisms that allow them to survive and reproduce, even in the presence of harmful agents. However, herbivory always has an impact on a plant's internal resource allocation dynamics. Whether this translates into impacts on fitness depends upon several internal and external factors. Plant resource allocation to vital functions varies, depending on species and environmental conditions (Bazzaz *et al.*, 1987; Yang *et al.*, 2016; Züst and Agrawal, 2017). Trade-offs between different functions, such as growth and defence, growth and reproduction or tolerance and defence have been documented (Leimu and Koricheva, 2006; Boege *et al.*, 2007; Züst and Agrawal, 2017). Furthermore, reproduction is a fundamental aspect in any plant's life cycle because it implies a strong resource investment (Wiens, 1984; Noordwijk and de Jong, 1986; Lovett Doust, 1989). Therefore, the way in which perennial individuals allocate their resources each year is fundamental in their entire life cycle.

Previous studies on herbivory have generally found a negative impact of herbivore damage on plant reproductive success and fitness (Dominguez and Dirzo, 1994; Koptur *et al.*, 1996; Strauss and Irwin, 2004; Boege, 2005*a*; Zvereva and Kozlov, 2014). However, there are some cases where such an effect has not been detected (Obeso and Grubb, 1993; Strauss *et al.*, 2001). Likewise, artificial damage is a method used in a wide variety of studies measuring the impact of herbivore damage on the numbers of flowers, seeds and fruits (Strauss, 1988; Mutikainen and Delph, 1996; Hjälten, 2008). Yet it has been found that the impacts can be different under natural and artificial herbivory (Baldwin, 1990; Lehtila and Boalt, 2008). In addition, a significant number of studies report a one-time estimate of damage, quantifying it with a single measure. This can lead to an underestimation of the effects of herbivory on reproduction (Coley and Barone, 1996). Due to different leaf time-spans among species, it is often impossible to know the time-scale over which damage has accumulated (Coley and Barone, 1996).

Male and female components of reproduction in both dimorphic and monomorphic plants are not always correlated or behave in parallel (Mutikainen and Delph, 1996). Consequently, by only considering the female component (fruits and seeds) when measuring plant fitness, we can under- or overestimate

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the reproductive success of plants. Moreover, there are accessory costs associated with herbivore damage. For example, tissues that do not strictly constitute the sexual whorls and/or embryo nourishment but are very important for attraction of pollinators or seed dispersers can be affected. Hence, reproductive costs are not limited to gametes and seeds (Wenk *et al.*, 2017). Peripheral elements enhancing plant reproduction, such as the size of the corolla, quantity of nectar and volatiles and so forth, tend to be negatively affected by foliar herbivore damage (Strauss *et al.*, 1996; Strauss, 1997; Suárez *et al.*, 2009; Lucas-Barbosa, 2016). Thus, if herbivory affects these aspects, it can also interfere with pollination success and/or seed dispersal, among other biotic interactions.

Abiotic factors also have a strong influence on species reproductive processes. In the case of tropical deciduous forests, water availability plays a vital role (Bullock and Solis-Magallanes, 1990; Lasky *et al.*, 2016; Cortés-Flores *et al.*, 2017) because there is highly marked rainfall seasonality . This stressing situation increases the pressure from herbivory, as growth and reproduction occur during a limited period. Furthermore, herbivore activity is constrained to the same short rainy season, being higher at the beginning of it (Dominguez and Dirzo, 1994; Filip *et al.*, 1995). Hence, changes in the amount of foliar damage during the rainy season are likely to have differential impacts at different phenological stages.

Tropical dry forest woody plants have developed a wide variety of strategies allowing them to survive marked seasonality, foliage loss during drought being the most evident adaptation (Reich and Borchert, 1984; Reich, 1995). However, there are other, less conspicuous, mechanisms, such as proleptic flowering (Borchert, 1983). In the first case, foliage senescence implies programmed cellular death (Taiz and Zeiger, 2010). In consequence, resources are moved from an organ to the central phloem, where they are reallocated for other functions and/or structures (Rentería *et al.*, 2005; Taiz and Zeiger, 2010; Rentería and Jaramillo, 2011). In proleptic species of tropical dry forests, flowering induction happens at the end of the rainy season, followed by a meristematic latency phase induced by drought, which is broken by the first rains in the following growing season (Borchert, 1983). The precise mechanics of the switch from vegetative to reproductive phase of the meristems in this particular type of tropical dry forest plants is not well understood yet. However, it is probably influenced by the interplay of endogenous and exogenous factors (Borchert, 1983, 2000), a situation that has been seen in proleptic shoots of different kinds of plants, such as almond trees (*Prunus dulcis*; Negrón *et al.*, 2014; Tombesi *et al.*, 2017). Nonetheless, for deciduous trees leaf senescence could play also a significant role (Borchert, 1983, 2000).

In this way, the amount of foliar damage suffered by a plant in a season has an impact on the resources reallocated during leaf senescence and what can be accumulated for the next season. This effect could be more marked in proleptic species, because the amount of foliar damage suffered will influence the meristem number in which the phase change is triggered, being reflected in the next season's flower number. In other words, the timing of resource availability and acquisition can be altered by leaf damage and reflected in reproductive success. We addressed this relationship among damage timing, resource availability and reproductive success with two piecewise structural equation models proposing a series of hypothetical causal relationships among herbivore damage and fitness components of *Casearia nitida*, a proleptic tropical dry forest tree (Table 1; Fig. 1A, B). We aim to investigate how foliar herbivore damage is related directly and indirectly to male and female reproductive characters. In addition, we assessed when herbivore damage has greater impacts on plant fitness.

MATERIALS AND METHODS

Study system

The present study was performed in the coastal region of Jalisco, Mexico, within the Chamela Biological Station (19°30′ N, 105°03′ W; UNAM), located in the Chamela-Cuixmala Biosphere Reserve (CCBR). The average annual precipitation is 800.4 mm (Maass *et al.*, 2018). Due to the marked seasonality, 86.8 % of the rain is concentrated between June and October (Bullock and Solis-Magallanes, 1990), with some scattered rains in December and January (IBUNAM, Estación Biológica de Chamela, 2016). The annual average temperature is 26.6 °C, with fluctuations up to 30.3 °C (IBUNAM, Estación Biológica de Chamela, 2016; Maass *et al.*, 2018). The vegetation is mostly deciduous forest, with small areas of semideciduous forest, aquatic vegetation of coastal lagoons, riparian vegetation, coastal dunes and xerophytic scrub (Noguera *et al.*, 2002).

Study species

Casearia nitida (Salicaceae) (von Jacquin, 1760; Alford, 2005) is a proleptic woody hermaphroditic plant between 2 and 6 m high, with a neotropical distribution (Alford, 2005; Global Biodiversity Information Facility, 2017). Vegetative and reproductive meristems activate after the first 10 mm of cumulated rain (June–July; Boege 2005*a*, *b*), breaking the latency phase induced by drought, a distinctive feature of the region, particularly in proleptic species (Borchert, 1983). The development of the inflorescences is almost immediate, around 10 d after meristem activation (Boege, 2005*a*). There are two major groups of floral visitors: dipterans (Bombyliidae and Stratiomyidae; pers. obs. E.N.Q.-P) and hymenopterans (Meliponini Apidae; pers. obs. E.N.Q.-P). Interestingly, for the related species *Casearia grandiflora* and *Casearia javitensis*, mostly dipterans (Syrphidae) have been reported as floral visitors (de Oliveira and Oliveira, 2000; Patricia *et al.*, 2010). The season's foliage is mostly produced at the beginning of the rainy season and takes ~2 weeks to completely expand (Boege, 2005*b*). During this period the greatest herbivore damage occurs. The rates of natural foliar damage oscillate between 15 and 20 % annually (López-Carretero, 2010; Ferreira, 2014). Herbivory is mainly caused by lepidopteran larvae (85 %), while orthopterans and coleopterans contribute 6 and 8.5 %, respectively, with most of the damage occurring in non-reproductive plants, which suffer 66 % more herbivory than reproductive individuals (Boege, 2005*a*). Fruits take around 2 months to mature, between August and September (Boege, 2005*a*, *b*); the dehiscent fruit changes colour from green to an intense yellow, with a red

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TABLE 1. *Hypothesized causal relationships among foliar herbivory, plant size, rainfall and reproductive characters of the proleptic tree* Casearia nitida. *Folivory$_{16cu}$ is the cumulated herbivore damage from 2016, Folivory$_{flo}$ is the herbivore damage occurring during the 2017 flowering period, and Folivory$_{fru}$ is the amount of damage during the fructification period. The superscripts refer to proposed mechanisms that also apply to other response variables*

Response Variable	Causal variables and expected effect (+/–)	Proposed mechanisms
Folivory$_{16cu}$	Plant height (–)[1]	[1]Size is a fundamental response to resource availability and competition (Goldberg *et al.*, 2017); there are also numerous structural factors that may change as trees grow (Boege *et al.*, 2011). Therefore, it is likely that larger plants are able to acquire more resources.
Folivory$_{flo}$	Plant height (–)[1] Folivory$_{16cu}$ (+)	During leaf senescence there is resource reabsorption and reallocation (Rentería *et al.*, 2005; Taiz and Zeiger, 2010); likewise, foliar damage has negative effects on plant fitness (Coley and Barone, 1996). So those plants with greater foliar damage will have substantial limitation in allocating the next season's reproduction and defence resources.
Folivory$_{fru}$	Plant height (–)[1] Folivory$_{flo}$ (–)	Plant resistance to foliar damage is subject to phenotypic plasticity, and many defence traits are expressed in the presence of harmful agents (Heil, 2002). Strong herbivore damage at the beginning of the season may induce defences in the foliage that remain for the rest of the season.
Inflorescence number	Plant height (–)[1] Folivory$_{16cu}$ (–) Folivory$_{flo}$ (–) Rainfall (+)[2]	It has been seen that leaf damage usually has negative impacts on plant fitness (Coley and Barone, 1996). In proleptic species the amount of foliar damage will influence the meristem number in which the phase change is triggered, and early damage will also impact the developing floral buds. [2]Flowers, like leaves, also lose water by transpiration (Liu *et al.*, 2017); therefore, a long dry spell during the flowering period could alter flower water balance, inducing death.
Flower number	Plant height (–)[1] Folivory$_{16cu}$ (–) Folivory$_{flo}$ (–) Rainfall (+)[2] Inflorescence number (+)	It has been seen that leaf damage usually has negative impacts on plant fitness (Coley and Barone, 1996). In proleptic species the amount of foliar damage will influence the meristem number in which the phase change is triggered, as well as the flower number that can develop from each meristem. Early damage will also impact the number of flowers reaching anthesis. With a higher number of floral meristems there will be a greater number of flowers, even if each inflorescence is sparse.
Synchrony	Rainfall (+)	Due to marked seasonality in tropical dry forests, there is a tight relationship between rainfall and flowering; furthermore, at the study site most of the species blossom during the first 2 months of the rainy season (Bullock and Solis-Magallanes, 1990).
Growth	Plant height (–)[1] Folivory$_{16cu}$ (–) Folivory$_{fru}$ (–) Flower number (+) Fruit number (–)	Biomass production requires resources (Lovett Doust, 1989); therefore, plants must allocate them with internal and external constraints for both types of meristem, vegetative and reproductive.
Infructescence number	Plant height (–)[1] Folivory$_{fru}$ (–) Inflorescence number (+) Synchrony (+)[3]	Strong herbivore damage after the total leaf expansion has negative effects on fruit production in this species (Boege, 2005*b*). Plants with greater numbers of inflorescences can develop as many infructescences as the number of inflorescences that are produced. [3]In plants requiring outcrossing, synchrony increases the number of possible mates (Kang and Bawa, 2003), and probably the number of sired infructescences, fruits and seeds.
Fruit number	Plant height (–)[1] Folivory$_{fru}$ (–) Infructescence number (+) Flower number (+) Synchrony (+)[3] Floral diameter (+)	With a higher number of reproductive meristems there will be a greater number of fruits, even if each infructescence is sparse. Plants with more flowers can develop as many fruits as the number of flowers that are produced. Fewer or smaller flowers can lead to a drop in floral visiting rates (Suárez *et al.*, 2009), thus reducing the probability of siring fruits and seeds.
Seed number	Plant height (–)[1] Folivory$_{fru}$ (–) Pollen number (–) Ovule number (+)	Even in hermaphrodite plants, some individuals can allocate a major reproductive effort to female or male fitness (Strauss *et al.*, 2001), through an increase in the production of female or male structures. Therefore, it is possible that the fitness of one sex or the other is more affected.
Floral diameter	Plant height (–)[1] Folivory$_{16cu}$ (–) Folivory$_{flo}$ (–) Flower number (–)	Foliar herbivore damage can impact diverse reproductive traits (Strauss *et al.*, 1996; Strauss, 1997), not only the number of reproductive structures produced. Allocating resources for reproduction goes beyond the number of activated meristems; the quality of each structure may also be affected. There is a trade-off tendency in quantity versus quality of flowers (Sargent *et al.*, 2007)
Pollen size	Plant height (–)[1] Folivory$_{16cu}$ (–) Folivory$_{flo}$ (–)	The non-linearity of female and male fitness may cause a differential impact of herbivore damage (Mutikainen and Delph, 1996), whereby male fitness can be affected negatively.
Pollen number	Plant height (–)[1] Folivory$_{16cu}$ (–) Folivory$_{flo}$ (–)	The non-linearity of female and male fitness may cause a differential impact of herbivore damage (Mutikainen and Delph, 1996), whereby male fitness can be affected negatively.
Ovule number	Plant height (–)[1] Folivory$_{16cu}$ (–) Folivory$_{flo}$ (–) Pollen number (–)	Even in hermaphrodite plants, some individuals can allocate a major reproductive effort to female or male fitness (Strauss *et al.*, 2001), through an increase in the production of female or male structures. Therefore it is possible that the fitness of one sex or the other is more affected.

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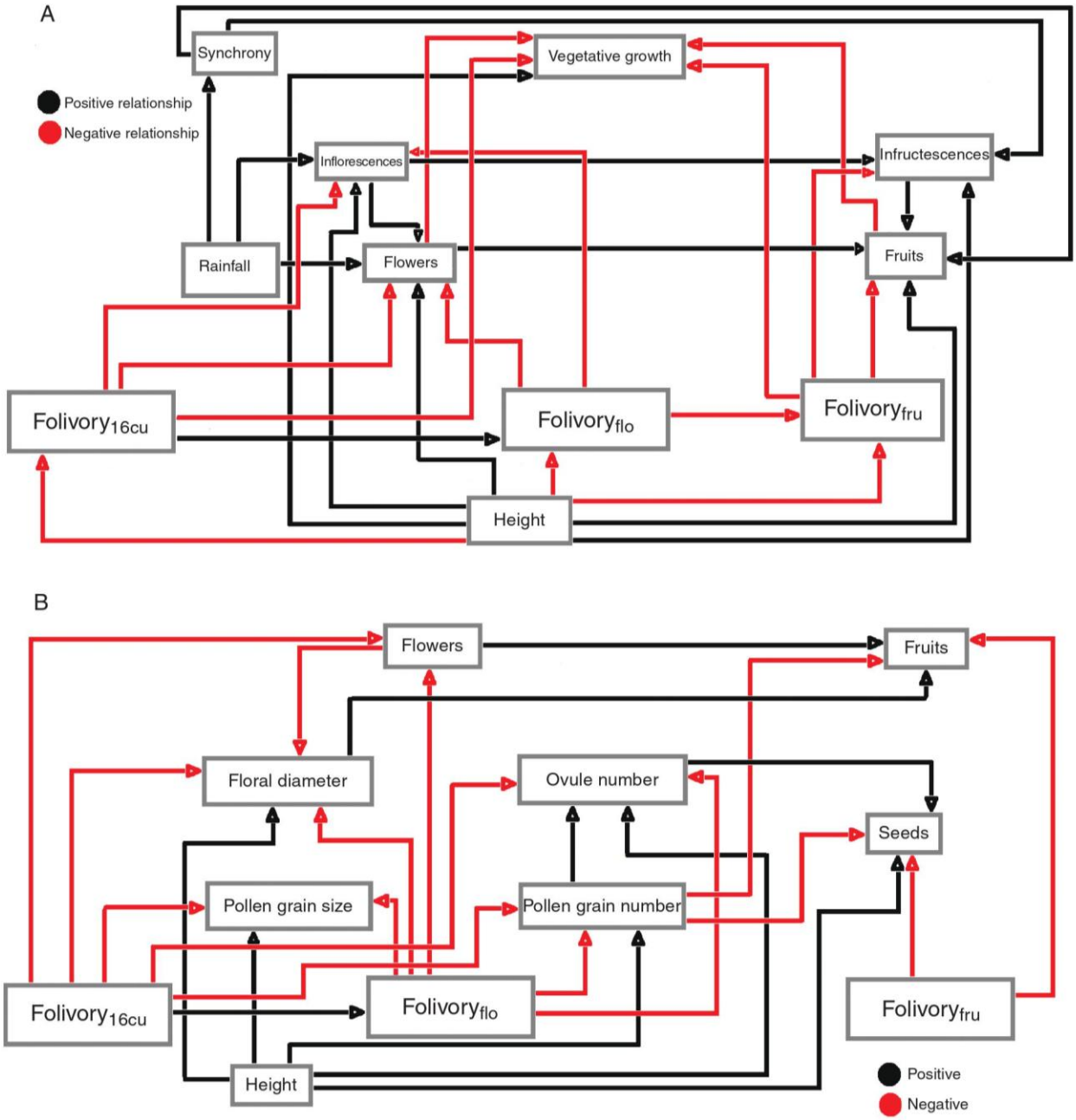

FIG. 1. Hypothesized causal relationships among foliar herbivory in different phenological stages and fitness traits in *Casearia nitida*. Boxes represent measured variables. Black and red arrows denote expected positive and negative relationships, respectively. Folivory$_{16cu}$ is the cumulated foliar herbivore damage from 2016, i.e. before flowering. Folivory$_{flo}$ is the foliar damage occurred during the 2017 flowering period. Folivory$_{fru}$ is the damage during the fructification period. Folivory may influence macro fitness traits like inflorescence number, flower number, vegetative growth, infructescence number and fruit number (A), but also micro fitness traits, both female (flower number, seeds, floral diameter and ovule number) and male (pollen grain size and pollen grain number) (B). Plant height may impact all biological traits. Rainfall could affect the number of reproductive structures produced (flowers, inflorescences, infructescences and fruits).

interior, probably dispersed by birds. At the end of the rainy season (November–December), *C. nitida* loses all its leaves (Boege, 2005*b*).

Herbivore damage assessment

In November 2016, before foliar senescence, three sites were selected, each with 16 adult plants of *C. nitida* ($N = 48$). Assessment of foliar herbivore damage (folivory) was done three times, corresponding to different phenological stages (Fig. 2). The first assessment was done at the beginning of November 2016 in senescent leaves, so it represents the cumulated herbivory from 2016 (hereafter Folivory$_{16cu}$). The second assessment was done in July 2017 on early-season leaves that develop during flowering (Folivory$_{flo}$). The last assessment was done in September 2017 during fructification (Folivory$_{fru}$).

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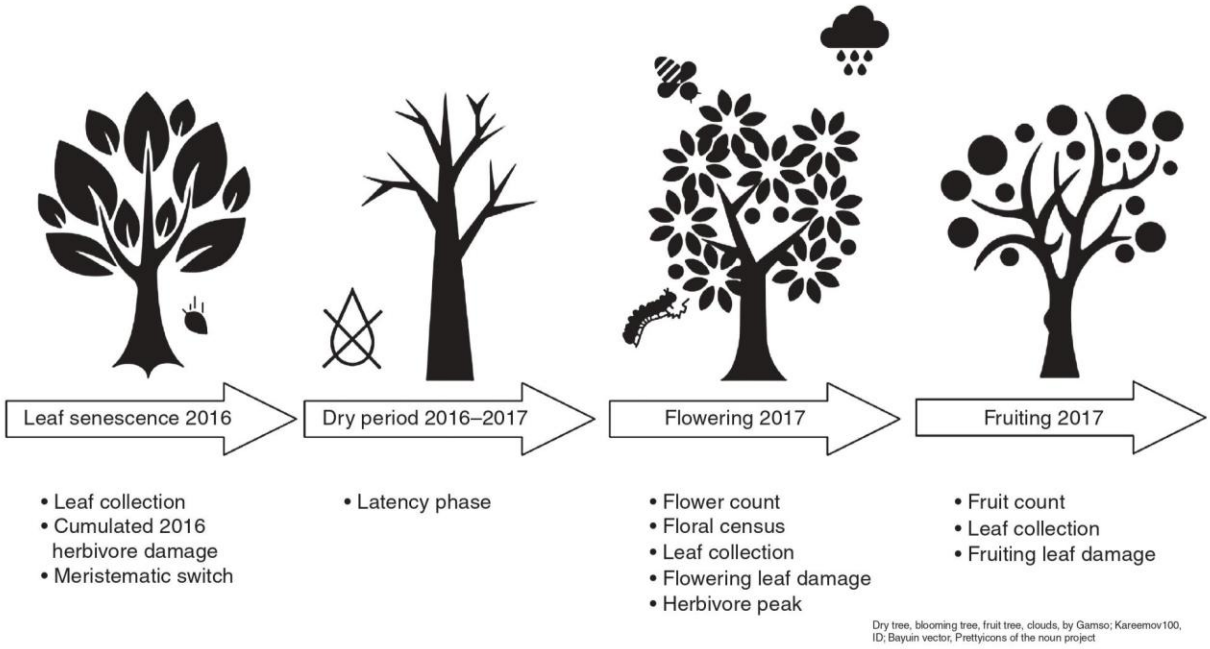

FIG. 2. Phenological state and time line.

In each assessment, 20 leaves per plant were systematically collected and then scanned to measure the remaining foliar area using ImageJ software (Schneider *et al.*, 2012). Afterwards, the total undamaged foliar area (A) was obtained using the equation [$A = 0.69\ (L \times W) + 0.79$, $R^2 = 0.99$, $F = 9652.9$, $P < 0.0001$] (Boege 2005*a*), where L corresponds to leaf length and W to leaf width. Folivory was then quantified as the percentage of foliar area loss.

Fitness

Fitness was evaluated using macro- and micro-scale traits (macro-scale traits do not require laboratory processing, whereas micro-scale traits do). To evaluate the effect of foliar damage on macro traits, 20 branches per plant were systematically marked in June 2017, and all inflorescences and infructescences that developed were counted. In each marked branch, a randomly selected immature inflorescence was marked in July 2017 and monitored daily, counting the number of open flowers per day until immature fruit formation. In September 2017 mature fruits in each marked inflorescence were counted, and the current season's branch growth was measured; the current season's growth is easy to distinguish due to clear differences in stem colour from other seasons.

For micro traits, up to 20 pre-anthesis and 20 anthesis flowers were collected in July 2017 on those plants with enough flowers, and up to 20 fruits per plant were collected in September 2017. Diameter of the flowers collected at anthesis was measured with a digital calliper (0.01 mm resolution) and ovule number of 15 anthesis and 15 pre-anthesis flowers per plant was counted. For pollen load, ten pre-anthesis flowers per plant were used; anthers were extracted and placed in microtubes with 100 µL of distilled water and a soap bean, and they were then ground with a dissection needle. Pollen grain counts were performed under a stereoscopic microscope (AmScope, 7×-45×). A 10-µL aliquot was placed on a microscope slide and, with the help of a 0.25 mm^2 grid, the number of pollen grains per sample was obtained. To estimate pollen grain size, a two-field photo was taken per sample (two squares of 0.25 mm^2) with an Olympus VR-320 camera. The equatorial diameter of each pollen grain was then calculated with ImageJ software (Schneider *et al.*, 2012). Finally, the number of seeds per fruit was counted for all collected fruits.

Additionally, a rough estimate of flowering synchrony among individuals was obtained by calculating how many conspecific trees in bloom coincided with each blooming tree per day. Also, the height of each plant was measured in order to control for variation induced by differences in age and size among individuals. Finally, to account for some of the environmental variation induced by the region (dry spells occurred during the flowering period), the cumulated number of millimetres of rain per day during *C. nitida*'s flowering period was used (IBUNAM, Estación Biológica de Chamela, 2016; Table 1).

Statistical analysis

We used piecewise structural equation models (SEMs) to test our hypotheses of causality between florivory and plant fitness, as represented in Fig. 1A, B. This method is used to evaluate hypotheses framed as a network of causalities, such that the variables included can enter as both predictors and responses, allowing identification of direct and indirect effects (Lefcheck, 2016; Shipley, 2016). Due to low flower production of some individuals, it was impossible to obtain complete information on floral diameter, ovule number, seed number, pollen number and pollen size for all individuals. Therefore, we decided to use two piecewise SEMs, the first one focused on macro traits

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(named 'major character analysis') using data from all individuals ($n = 48$; Fig. 1A), and the second one focused on micro traits (named 'smaller character analysis') employing a reduced data set ($n = 31$ Fig. 1B). This allowed us to reduce the complexity of a full model, enhancing the clarity of the multiple proposed relations, and the robustness of the analyses.

Piecewise SEM fitting was done following Shipley (2016) and using several dependencies of the R statistical language (R Core Team, 2019). First, for each response (endogenous) variable in Fig. 1A, B we fitted a linear mixed model including as predictors those variables from which they get an effect (as defined by an incoming arrow), and site as random effect on the intercept (all the models fitted, distributions assumed and particular R functions used are available in Supplementary Data Appendix S1). All variables were previously standardized to obtain standardized path coefficients, which allow further comparisons of the magnitude of relationships. The conditional coefficient of determination (R_c^2) for each linear mixed model was calculated. Then, we assessed the overall fit of the model using Fisher's C test (Shipley, 2016), which essentially tests the existence of relevant relationships among variables not included in the original hypothesis, i.e. missing paths. Such a test required fitting a second set of linear mixed models, which are defined by a set of conditional independence claims inferred from the original hypotheses (Fig. 1A, B) and jointly called the basis set. Details of the models included in each basis set are also provided in Supplementary Data Appendix S1.

RESULTS

Analysis of major characters: first structural analysis

The models in this analysis show a large influence of herbivory on reproductive traits; many of these models explained a large part of the variance (R_c^2). The response variables showing higher percentages of explained variation were the numbers of inflorescences and infructescences per branch, open flowers, mature fruits and synchrony (Fig. 3). Folivory_{16cu} (mean ± s.d. 13.5 ± 4 %) had a larger negative impact on the inflorescence number per branch (standardized $\beta = -0.350$, $P = 0.008$) than on the open flower number (standardized $\beta = -0.006$, $P = 0.005$). Also, Folivory_{16cu} showed a positive relationship with Folivory_{flo} (mean ± s.d.; 30 ± 4 0%, standardized $\beta = 0.326$, $P = 0.012$). In contrast, Folivory_{flo} showed a positive relationship with the number of

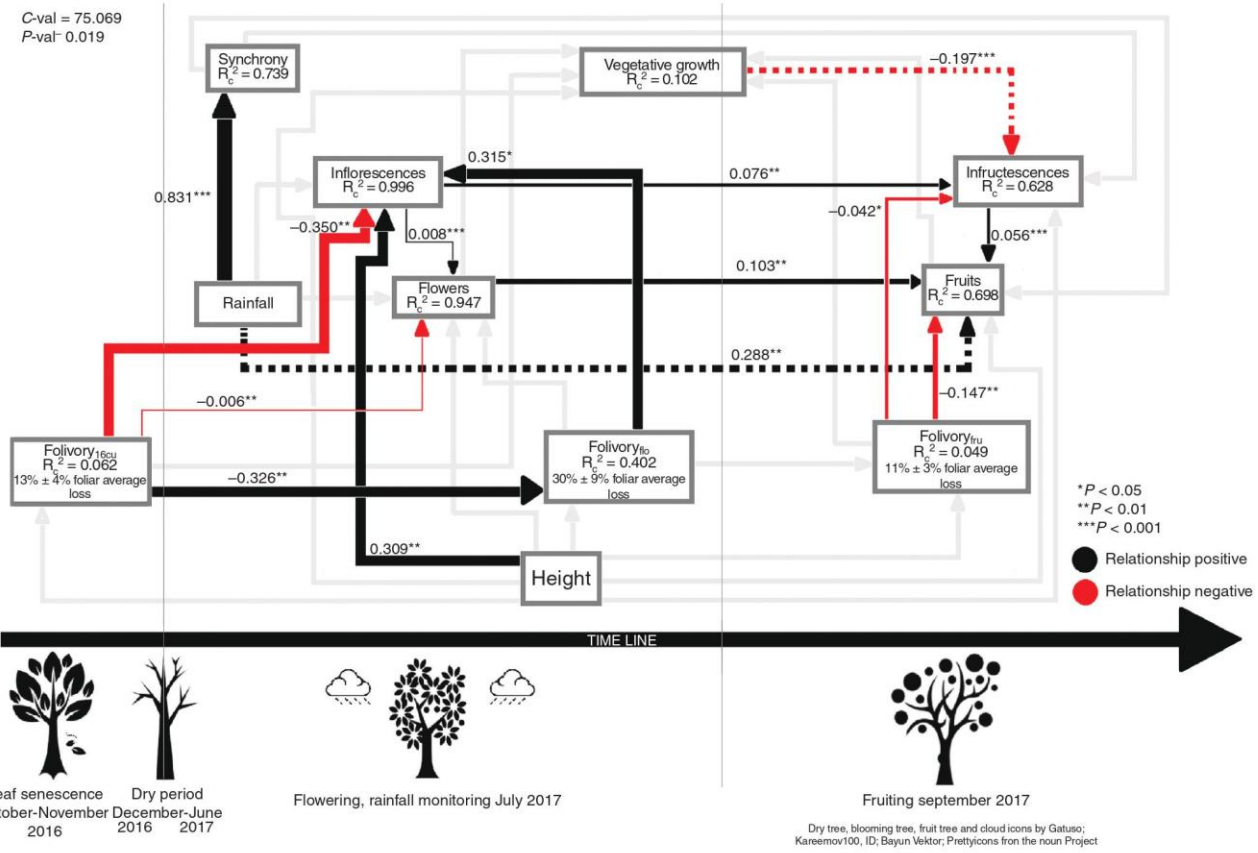

FIG. 3. Analysis of major characters: first structural analysis. Boxes represent measured variables. Arrows represent unidirectional relationships among variables. Black arrows denote positive relationships and red arrows negatives ones. Semitransparent arrows indicate non-significant paths ($P < 0.05$) that were included in the *a priori* model. Dotted arrows indicate the found missing paths (not included in the *a priori* model). The thickness of an arrow is proportional to its effect size. R_c^2 values for component models are given in the boxes of response variables (reported as the conditional based on the variance of both the fixed and random effects). Magnitude coefficients and significance thresholds are shown along paths. The temporal axis is located below with marked sections for each evaluated phenological moment.

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inflorescences per branch (standardized $\beta = 0.315$, $P = 0.031$). For overall effects including indirect routes see Table 2.

Folivory$_{fru}$ (mean ± s.d.; 11 ± 3 %) showed a negative impact both on the number of infructescences per branch (standardized $\beta = -0.042$, $P = 0.018$) and on fruit number (standardized $\beta = -0.147$, $P = 0.004$), with the latter being the greatest effect (for overall effects including indirect routes see Table 2). Plant size (height) was positively related to inflorescence number (standardized $\beta = 0.309$, $P = 0.005$). As expected, there were evident significant relationships among the numbers of flowers, inflorescences, fruits and infructescences, as well as precipitation and floral synchrony (significance level in Table 3; full models in Supplementary Data Appendix S1).

The piecewise SEM missing paths showed two significant relationships (Fig. 3, dashed arrows): a negative relationship between growth and the number of infructescences per branch, and a positive relationship between precipitation during flowering and fruit number. Therefore, due to the presence of this significant missing path, when calculating Fisher's *C* statistic the complete model is rejected ($C = 75.069$, d.f. = 52, $P = 0.019$). In other words, this low *P* value implies the existence of missing relationships among unconnected variables.

Analysis of smaller characters: second structural analysis

In this analysis the impacts of herbivory on fitness traits were directly negative and with fewer alternative paths (for overall effects including indirect routes see Table 2). A lower variance percentage (based on R_c^2; compared with the first SEM) is explained by the models integrating it; only three response variables yielded an R_c^2 over 50 % (Fig. 4). Folivory$_{16cu}$ had a strong negative relationship with pollen grain number per flower (standardized $\beta = -0.445$, $P = 0.006$), and with the number of flowers (standardized $\beta = -0.006$, $P = 0.000$), although of smaller magnitude. Additionally, Folivory$_{16cu}$ was positively related to Folivory$_{flo}$ (standardized $\beta = 0.363$, $P = 0.028$).

Folivory$_{flo}$ showed a strong negative effect on pollen grain size (standardized $\beta = -0.406$, $P = 0.032$) and Folivory$_{fru}$ had a negative impact on seed number (standardized $\beta = -0.463$, $P = 0.012$). At the same time, pollen grain number showed a negative relationship with seed number (standardized $\beta = -0.430$, $P = 0.002$). Floral diameter had a positive impact on mature fruit number (standardized $\beta = 0.254$, $P = 0.000$), while the number of flowers had a positive effect on fruit number (standardized $\beta = 0.146$, $P = 0.005$). Finally, height and ovule number did not show significant relationships with any of the proposed variables.

This model showed four significant missing paths (Fig. 4, dashed arrows): floral diameter had a strong negative impact on seed number and, to a lesser extent, on Folivory$_{fru}$; ovule number had a negative relationship with Folivory$_{fru}$ while flower number had a strong positive impact on ovule number; and finally, due to the presence of four missing paths, Fisher's *C* statistic yielded a low *P* value ($C = 91.357$, d.f. = 52, $P = 0.011$). Thus, the model was rejected. As we mentioned before, this implies the existence of missing relationships among unconnected variables.

Overall effects of herbivore damage

Unifying the results of both analyses, Folivory$_{16cu}$ had the largest effect on the reproductive success of *C. nitida*, affecting more characters than the other two evaluated damages (Folivory$_{flo}$, Folivory$_{fru}$). The previous season's herbivore damage (Folivory$_{16cu}$) had a large impact on the next season's reproductive characters, both directly and indirectly. Furthermore, the impact was negative on all reproductive traits, except for seed number, which was indirectly affected positively. As far as we know, this outcome has not been reported for any proleptic species or time lapse. In addition, Folivory$_{16cu}$ had another positive relationship with Folivory$_{flo}$, indicating that plants with most damage in 2016 also suffered grater herbivory during the next season's flowering period. Nonetheless, this last estimate had a lesser impact on fitness components, despite being the largest percentage (30 ± 9% missing foliar area). Directly, Folivory$_{flo}$ had two important effects, a positive one on the inflorescence number and a negative one on pollen grain size. Indirectly the influence was positive on several characters but very low, generating an indirect compensatory effect on the numbers of flowers, infructescences and fruits. However, given the negative influence of the other two estimated amounts of foliar damage, the effect was probably cancelled or diluted. Folivory$_{fru}$ had direct negative impacts on all the studied variables, except for vegetative growth, and its influence was stronger on the number of seeds in spite of being the smallest percentage of herbivore

TABLE 2. *Overall effects of herbivore damage at different phenological stages on reproductive traits. Includes direct and indirect effects from herbivore damage obtained by multiplying each coefficient path per route trait, and adding alternative routes for the same trait*

Affected trait	Overall effect Folivory$_{16cu}$ magnitude (β)	Overall effect Folivory$_{flo}$ magnitude (β)	Overall effect Folivory$_{fru}$ magnitude (β)
Major character analysis (SEM1)			
Inflorescences	−0.2480	0.3150	–
Flower number	−0.0070	0.0025	–
Infructescence number	−0.0180	0.0230	−0.0420
Fruit number	−0.0007	0.0002	−0.1447
Smaller character analysis (SEM2)			
Flowers	−0.0060	–	–
Fruit number	−0.0008	–	–
Pollen grain size	−0.1470	−0.4060	–
Pollen grain number	−0.4450	–	–
Ovule number	−0.0039	–	–
Seed number	0.1910	–	−0.4630

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TABLE 3. *Manifest relationships among flowers and fruits from first structural equation model (major characters). For complete models see Supplementary Data Appendix S1*

Related variables			Significance ($P \leq 0.05$)	Standardized β (magnitude)
Inflorescence number	→	Flower number	0.000	0.008
		Infructescence number	0.001	0.076
Flower number	→	Fruit number	0.009	0.103
Infructescence number	→	Fruit number	0.000	0.056
Precipitation	→	Synchrony	0.000	0.831

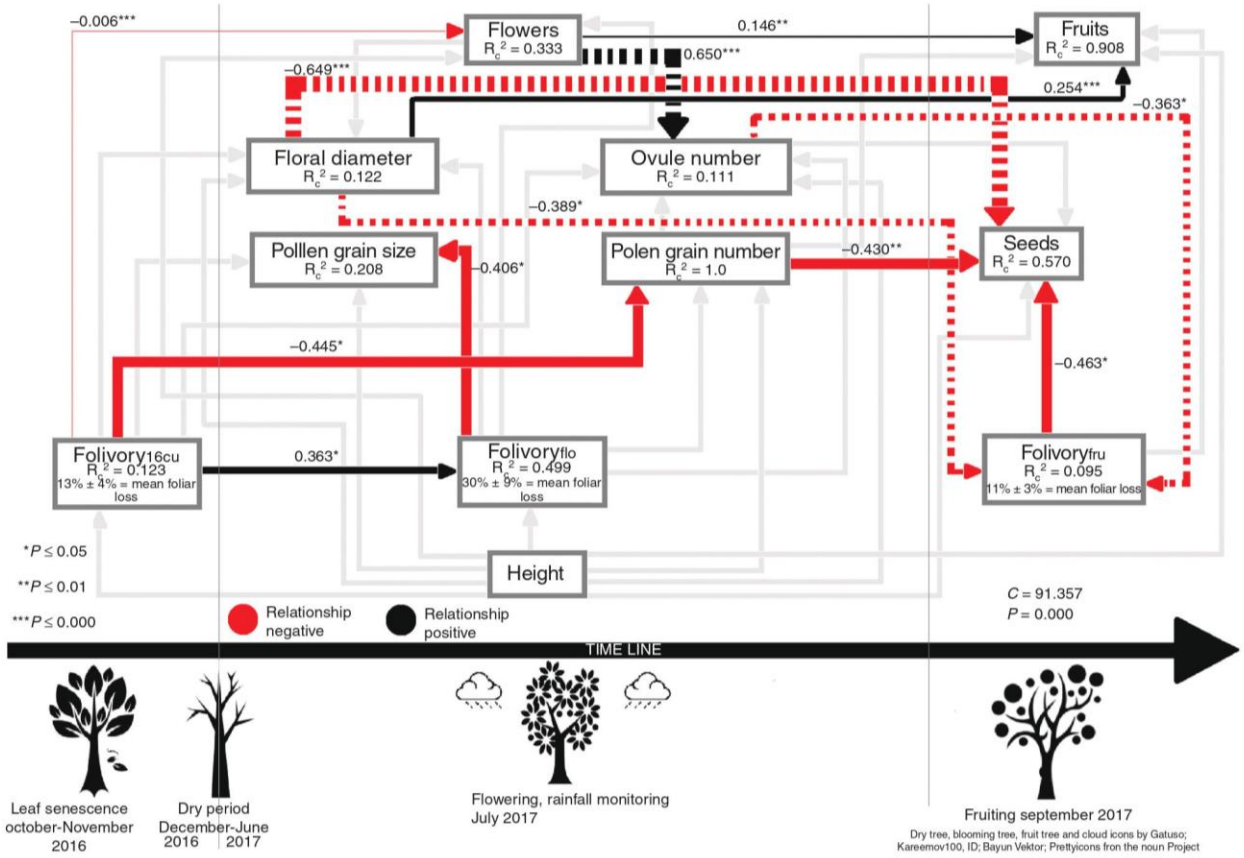

FIG. 4. Analysis of smaller characters: second structural analysis. Boxes represent measured variables. Arrows represent unidirectional relationships among variables. Black arrows denote positive relationships and red arrows negatives ones. Semitransparent arrows indicate non-significant paths ($P < 0.05$) that were included in the *a priori* model. Dotted arrows indicate the found missing paths (not included in the *a priori* model). The thickness of an arrow is proportional to its effect size. R_c^2 values for component models are given in the boxes of response variables (reported as the conditional based on the variance of both the fixed and random effects). Magnitude coefficients and significance thresholds are shown along paths. The temporal axis is located below with marked sections for each evaluated phenological moment.

damage (11 ± 3%). Both analyses point towards a general negative effect of herbivore damage on reproductive success, as well as a division in resource allocation between the previous season's cumulated resources and those produced the following season, which suggests a conflict between allocation to defence mechanisms against herbivory and allocation to reproduction.

Descriptive statistics of traits

Herbivore damage estimates showed similar variation when the standard deviation was analysed (Table 4). Folivory$_{flo}$ presented higher variation and Folivory$_{fru}$ the lowest; however, when taking into account the ratio of the standard deviation to the mean [coefficient of variation (CV), Table 4], Folivory$_{flo}$ showed lower dispersion and Folivory$_{16cu}$ the greatest. Nonetheless, the three measures had similar dispersion. Of the fitness traits used here, floral diameter, ovule number and pollen grain size had lower levels of variation (s.d. and CV, Table 4), whereas vegetative growth, synchrony, height and pollen grain number had intermediate levels of variation (s.d. and CV, Table 4). Finally, the traits with greater levels of dispersion were the numbers of inflorescences, flowers, infructescences, fruits and seeds (s.d. and CV, Table 4). However, the last three characters should be

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Table 4. *Dispersion measures for foliar damage estimates and fitness traits*

	Mean	s.d.	CV
First structural analysis			
Folivory$_{16cu}$ (%)	13.577	4.967	0.365
Folivory$_{flo}$ (%)	30.040	9.404	0.313
Folivory$_{fru}$ (%)	11.522	3.730	0.323
Inflorescence number	104.9	92.401	0.880
Flower number	59.68	58.778	0.984
Fruit number*	1.809	3.366	1.861
Infructescence number*	5.468	14.054	2.570
Synchrony	211.8	105.631	0.498
Height (cm)	326.4	115.563	0.354
Vegetative growth (cm)	9.685	3.634	0.375
Second structural analysis			
Floral diameter (mm)	7.438	0.679	0.091
Pollen grain number	788.791	328.757	0.416
Pollen grain size (µm)	26.345	2.818	0.106
Ovule number	22.899	4.211	0.183
Seed number*	1.034	1.070	1.035

*Zero inflated variables.

approached with caution as they are variables with an excess of zeros. Nonetheless, this condition was taken into consideration when the linear mixed models for these traits were adjusted using zero-inflated models (Supplementary Data Appendix S1).

DISCUSSION

The results obtained in the present study indicate that the dynamics of resource acquisition and allocation patterns for reproduction lead to herbivore damage effects extended by longer periods than a single growing season (Figs 2–4). This acquisition–allocation–damage synergy can be expressed in complex ways, as is the case for *C. nitida*.

Herbivory effects on flowers and inflorescences

The negative impact of Folivory$_{16cu}$ on *C. nitida* female fitness was greater on inflorescence number than on flower number. This decrease could be due to florivory (i.e. damage to flowers), which was observed in the field but was not quantified in the present study. Nonetheless, the general negative impact of Folivory$_{16cu}$ can be explained by the proleptic nature of the species. Because the meristematic change from vegetative to reproductive state happens at the end of the previous growing season, when foliage senescence occurs (Borchert, 1983), foliar damage at this moment is high enough to reduce the available resources at the time of meristematic differentiation. Hence if foliar damage at this moment is high enough to reduce the available resources at the time of meristematic differentiation, there is a direct negative effect of herbivore damage on the meristem number, translated into the inflorescences number developing the following season, after the growth-induced latency during the dry season. This effect has been reported in the only other proleptic species in which the relationship between herbivory and fitness has been studied: *Erythroxylum havanense* (Dominguez and Dirzo, 1994). However, negative impacts of herbivore damage on flower production have been widely reported in other perennial species, like the hermaphroditic shrubs *Datura wrightii* and *Vaccinium ashei* (Lyrene, 1992; Elle and Hare, 2002; Lehndal *et al.*, 2016). Even in unisexual flower species (monomorphic and dimorphic systems) the number of flowers from a particular sex can be reduced after herbivore damage (Narbona and Dirzo, 2010; Litto *et al.*, 2015).

The most damaged plants in 2016 also received greater damage in 2017 (Fig. 3). It appears that defence/resistance variation and damage susceptibility in *C. nitida* individuals is maintained throughout time, and it is probably reflected in plant fitness differences (Underwood, 2012; Barker *et al.*, 2019). Boege (2005*b*) found that *C. nitida* defence compounds (phenols and tannins) diminish with increasing damage in reproductive and non-reproductive plants; however, a study evaluating defence maintenance as well as the influence of genotype through extended periods of time is lacking.

In *C. nitida* reproductive plants, the first developing leaves (those flushed along with the inflorescences) are considerably smaller than the rest of the foliage produced subsequently. Furthermore, it is known that young leaves are more attractive to herbivores despite being more defended (Bazzaz *et al.*, 1987; Coley and Barone, 1996). This short-lived foliage matches the highest herbivore activity (Filip *et al.*, 1995; Juan-Baeza *et al.*, 2015), explaining the high percentage of damage and probably the positive correlation with Folivory$_{16cu}$, due to a high investment in phenols and tannins (Boege, 2005*a*). Therefore, those plants that are more depleted the previous season would have a smaller energetic reservoir for defences the next season. There are also alternative explanations to the observed association between foliar damage levels across time: the density of herbivores may vary across locations or the quality of the food may vary across individuals due to physiological or genetic differences.

Contrary to our expectations, Folivory$_{flo}$ had a positive impact on the inflorescence number per branch, probably because herbivores consume the plant's new buds, damaging floral and vegetative meristems simultaneously. Plants are likely to compensate for this loss by activating additional meristems (Tuomi *et al.*, 1994; Buchanan, 2015; Nakahara *et al.*, 2018), creating a compensatory effect through inflorescence production (Wise *et al.*, 2008; West and Louda, 2018). Nonetheless, a more detailed study is necessary to see if this increase in inflorescences is reflected in progeny number, and if it is capable of buffering the negative impacts of Folivory$_{16cu}$ and Folivory$_{fru}$ on inflorescences, flowers, infructescences, fruits and seeds.

Herbivory effect on fruits and infructescences

Folivory$_{fru}$ is exerted on the foliage that expands days after flowering is over, when herbivore activity slightly decreases. Moreover, these leaves are synchronously flushed and develop quickly, hardening in few weeks, and there is an increase in resistance, explaining the decrease in foliar damage percentage (11 ± 3%). These leaves last for the rest of the season, and there is little replacement afterwards (Boege, 2005*a*).

Differences in the effects of leaf damage as a function of the phenological stage indicate that flowers and fruits rely on different resources (Dominguez and Dirzo, 1994). In the case of

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flowers, resources are accumulated during the entire previous season, while fruits require photosynthates produced during fruit maturation, as has been observed in *E. havanense*, another proleptic species of the region (Dominguez and Dirzo, 1994).

The negative impacts of herbivore damage occurring between the end of flowering and fruit maturation have been reported for *C. nitida* (Boege, 2005*a*) and for *E. havanense* (Dominguez and Dirzo, 1994). In general, there is a negative effect of defoliation in many plants (Stephenson, 1980; Koptur *et al.*, 1996; Mothershead and Marquis, 2000; Gong and Zhang, 2014), although there are exceptions (Obeso and Grubb, 1993; Agrawal, 2000). Nonetheless, the experimental designs of a large majority of studies use artificial defoliation treatments, as well as pre-established damage percentages. Though this makes it possible to control the variation induced by external factors, it has been reported that the effect can differ between natural and artificial damage (Baldwin, 1990; Tiffin and Inouye, 2000; Inouye and Tiffin, 2003). In the present study, similar results were obtained under natural herbivory, even with much lower amounts of foliar damage than those previously reported for artificial damage on *C. nitida* (Boege, 2005*a*) and other proleptic species (Dominguez and Dirzo, 1994). For example, a compensatory effect has been described in *C. nitida* at 25 % artificial foliar damage after flowering (i.e. fruiting foliage; Boege, 2005*b*), while in the present study this effect was detected only in the flowering foliage, with low indirect compensatory effects on infructescences and fruits (Table 2).

Effect of herbivory on male and female gametes

There were negative effects of $Folivory_{16cu}$ on the number of pollen grains per flower. Plants with greater levels of damage showed 24.1 % fewer pollen grains than plants with low damage. Studies evaluating defoliation effects on male function are relatively scarce. A negative tendency has been observed both in plants with unisexual flowers, like *Cucurbita texana* (monoic) or *Silene latifolia* (dioic; Quesada *et al.*, 1995; Litto *et al.*, 2015), as well as in some hermaphrodites such, as *Raphanus raphanistrum* (Strauss *et al.*, 1996; Lehtila, 1999). In proleptic species, as far as we know, this study constitutes the first report on this negative effect. A decrease in pollen production represents a drop in ovule-fertilizing probability; likewise it can affect pollinator attraction, reducing the probabilities of outcrossing (Frazee and Marquis, 1994; Quesada *et al.*, 1995; Strauss *et al.*, 1996; Lehtila, 1999; Parra-Tabla and Herrera, 2010).

Following the temporal axis, $Folivory_{flo}$ had also a negative impact on pollen grain size. This trait has proven to be a very stable character in other species, so this negative effect has only been observed in few studies investigating male fitness and herbivory (Strauss *et al.*, 1996; Lehtila, 1999). Even though it is known that herbivory rates change through time (Baldwin, 1990; Filip *et al.*, 1995), the impacts of damage temporality on reproductive success, particularly on male fitness components, has been scarcely assessed. However, it has been found that the effect of herbivore damage on reproduction is differential according to the season when defoliation occurs (García and Ehrlén, 2002). In the present study the impact on male and female characters varied as a function of the season in which herbivore damage occurred. This result suggests that development and supply of pollen grains is influenced by both the season's first photosynthates and the previous season's cumulated resources. In *Cucurbita texana* the flower's closest leaf has an impact on the development and supply of photosynthates for male structures (Quesada *et al.*, 1995). Hence, for *Cesiaria nitida*, while most resources for reproductive structures come from the previous season's storage, flowering foliage can be important for the tapetum and for pollen grain photosynthate supply. Further detailed studies are needed to determine if this size effect is reflected in pollen grain performance.

The ovule number was not directly affected by leaf damage at any time, only indirectly through the effect from $Folivory_{16cu}$ on flowers and probably inflorescences (if we consider the positive linear relationship between these last two from the first analysis). This suggests that there is a resource reserve assigned to the production and supply of female gametes. This lack of effect has been observed in species like the hermaphrodite shrub *Raphanus raphanistrum*, where ovule size and number were not affected by foliar herbivore damage (Lehtila, 1999), as reported also for other monoic and dioic species for female flowers (Narbona and Dirzo, 2010; Litto *et al.*, 2015). Nonetheless, there are isolated cases, such as *Chamaecrista fasciculata*, where there is a decrease in ovule size and number as a result of foliar damage(Frazee and Marquis, 1994).

Effect on seeds

$Folivory_{fru}$ showed a direct negative effect on seed number, a situation commonly reported (Stephenson, 1980; Dominguez and Dirzo, 1994; Niesenbaum, 1996; García and Ehrlén, 2002; Lehndal *et al.*, 2016); this suggests that these structures depend on the photosynthates produced during the season, in accordance with what has been recorded for *E. havanense* (Dominguez and Dirzo, 1994). Many perennials invest most of their reproductive effort in attraction structures, more than in seed production per reproductive cycle (Wenk and Falster, 2015; Wenk *et al.*, 2017). In such a way, we can see that temporary patterns of resource allocation in the plant have an influence on the progeny produced, where herbivory is able to interfere in these patterns (Bazzaz *et al.*, 1987; Strauss and Irwin, 2004; Lucas-Barbosa, 2016). Interestingly, $Folivory_{16cu}$ had a positive indirect effect on seed number through its negative influence on pollen grain number. This relationship suggests that a decrease in pollen grain number per flower can promote greater seed number and vice versa. This could indicate that certain individuals invest larger quantities of resources via masculine characters, while others do it through female fitness. A situation very similar to this case was proposed for *Raphanus raphanistrum*, where plants with more herbivore damage produced greater numbers of flowers (therefore more anthers and pollen grains) but no more seeds (Strauss *et al.*, 2001).

Other effects and missing paths

For both models we found missing paths, leading to model rejection. However, the core of our hypothesis, i.e. that the timing of herbivory is important, with its effects extending

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beyond the current season and thus affecting different additional fitness components, is sustained by the significant paths found, as previously discussed. Nonetheless, missing paths suggest relevant mechanisms that will require further research. The negative relationship between vegetative growth and the number of fruits per branch suggests a possible trade-off between the allocated resources for infructescences and those for vegetative growth; hence there must be limiting resources for these two characters (Bazzaz *et al.*, 1987; Calvo, 1993; Fridley, 2017). Similarly, the unexpected correlation between precipitation during flowering and fruit number suggests that those individuals that bloomed on days of higher precipitation were capable of maintaining more hydrated foliage. A greater photosynthetic rate would in turn maintain a greater quantity of fruits, as the water level in leaves changes through the season, being higher at the beginning (73.2 %) and decreasing towards the end of the season (57.9 %; Boege, 2005*b*). Delayed effects of precipitation on plant demographic rates have been demonstrated for seedlings in the same study region (Maza-Villalobos *et al.*, 2013, Martínez-Ramos *et al.*, 2018). Finally, negative missing paths detected on male and female gamete analysis could be incorporated into the model as correlation errors among variables and not considered causal (Bitenc *et al.*, 2017). The analyses showed that floral characters mostly depend on the resources accumulated during the previous season, while fruits depend on those produced in the current season. This does not imply, however, that the use of resources of both previous seasons' stock and next season's photosynthates are disassociated, and it could be that an excessive investment in floral characters (diameter and ovules) commits further energy allocation to embryos and defence.

Conclusions

Although previous studies on herbivory and plant reproductive success had an upsurge during the 1980s and 1990s, we are still trying to understand the factors contributing to the final outcomes of the interaction between herbivores and their hosts. In the present study, we included a wide array of fitness components to assess the temporal impacts of herbivore damage on a perennial deciduous plant. We demonstrated that cumulative herbivore damage during one season affected the next season's reproductive characters, in addition to the impacts that damage during flowering or fruiting can have on both female and male fitness. This kind evidence calls for attention and highlights the relevance of visualizing the relationships among different reproductive variables to understand how they are influenced by the seasonality of herbivore damage. Long-term studies including the study of different environmental variables and interacting species, such as pollinators and seed dispersers, can further contribute to our understanding of the dynamic impacts of herbivores on proleptic perennial species.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Appendix S1: endogenous variable models and basis set models for major and smaller character path analysis.

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DISCUSIÓN

Los resultados obtenidos en este estudio indican que la dinámica de adquisición de recursos así como los patrones de asignación de los mismos para la reproducción, generan que los efectos del daño producido por los herbívoros se extiendan por periodos mayores a una temporada reproductiva (Figs. 2, 3, 4). Esta sinergia en la adquisición-asignación-daño puede expresarse en formas complejas como es el caso de *C. nitida*.

***Efectos generales de la herbivoría*-**Unificando los resultados de ambos análisis (características de cada variable en anexo S2), el daño foliar acumulado de 2016 tuvo el mayor impacto en éxito reproductivo de *C. nitida*, afectando más caracteres que las otras dos estimaciones de daño foliar (daño foliar durante floración y daño foliar durante la fructificación). El daño foliar acumulado de 2016 tuvo un alto impacto en los caracteres reproductivos de la siguiente temporada lluviosa, tanto directa como indirectamente, incluso el efecto fue negativo en todas las variables relacionadas, con excepción del número de semillas, donde fue indirectamente positivo. Este resultado hasta donde se sabe, constituye el primer reporte de su tipo para especies prolépticas. Así mismo se observó una relación positiva con el daño foliar ocurrido durante la floración de la siguiente temporada, de tal manera que las plantas más dañadas en 2016 también sufrieron un mayor daño durante la floración de 2017. No obstante la herbivoría foliar ocurrida durante la floración presentó un impacto bajo en los componente evaluados, aún cuando es el porcentaje más alto de daño foliar (30% ± 9%). Directamente el daño foliar tuvo dos efectos importantes, uno positivo en el número de inflorescencias y uno negativo en el tamaño del grano de polen. Indirectamente generó un efecto compensatorio de baja magnitud en el número de flores, infrutescencias y frutos (Tabla 2). Sin embargo, dado el efecto negativo de los otros estimados de daño foliar, es posible que el efecto compensatorio esté diluido o cancelado. El daño foliar ocurrido durante la fructificación presentó un impacto negativo en todas las variables propuestas, excepto con el crecimiento vegetativo el cuál no se vio afectado por ninguna herbivoría. La herbivoría durante el periodo de fructificación tuvo una fuerte influencia en el número de semillas pese a ser el menor porcentaje de daño foliar (11% ± 3%). Ambos análisis apuntan a un efecto negativo general sobre el éxito reproductivo, así como a una división en la asignación de recursos, entre los acumulados la temporada anterior y aquellos producidos a la siguiente, lo que lleva a un conflicto entre la asignación de recursos a mecanismos de defensa contra herbívoros vs. recursos para la reproducción.

Efecto sobre flores e inflorescencias- El daño foliar acumulado del 2016 tuvo un impacto negativo sobre la adecuación femenina de *Casearia nítida*. Con un mayor efecto en el número de inflorescencias que en el de flores, probablemente por la influencia de la florivoría, la cual fue observada en campo pero no fue contabilizada en el presente estudio, este daño floral puede afectar la sobrevivencia de las mismas. Sin embargo en general el efecto negativo puede explicarse por la naturaleza proléptica de la especie, ya que el cambio del estado vegetativo al reproductivo del meristemo se da al final de la temporada lluviosa, junto con la senescencia del follaje, posteriormente viene un periodo de latencia inducido por sequía (Borchert 1983) que es roto por los primeros milímetros de lluvia acumulados (Boege 2005a). De tal manera hay una consecuencia directa de la herbivoría sobre el número de meristemos en los que se da la inducción a la floración y por lo tanto el número de inflorescencias que se desarrollarán la siguiente temporada. Este efecto también se observó en la única otra especie proleptica de la que sabemos se haya estudiado herbivoría y adecuación (*E. xavanense;* Dominguez and Dirzo 1994), no obstante, también se ha reportado esta disminución de flores en muchas otras especies de características diferentes como es el caso de *Datura wrightii* (Lyrene 1992; Elle and Hare 2002; Lehndal *et al.* 2016), incluso en especies de flores unisexuales se ha visto que puede impactar negativamente a las flores de algún sexo en particular (Narbona and Dirzo 2010; Litto *et al.* 2015).

Las canículas observadas en la región durante el estudio, tuvieron un efecto fuerte sobre la floración, aunque no hubo una relación significativa entre precipitación y número de flores. En campo se observó un marcado marchitamiento en varios individuos durante la canícula más larga. Ocurrida en el periodo de floración (8-15 de Julio), lo cual indica que para detectar los efectos de la precipitación en el despliegue floral, se requiere otra aproximación para la obtención de datos más robustos, probablemente a través del balance hídrico de la planta.

Adicionalmente hubo una correlación positiva entre el daño foliar acumulado de 2016 y el daño foliar durante la floración de 2017. Esto permite suponer que existe una variación en la defensa y suceptibilidad al daño en los individuos de *C. nitida* que se mantiene a través del tiempo, reflejándose probablemente en la adecuación de las plantas (Underwood 2012; Barker *et al.* 2019). Sin embargo es necesario un estudio que evalúe el mantenimiento de la defensa en periodos prolongados de tiempo.

En las plantas reproductivas, el follaje inicial que se desarrolla con las inflorescencias no es el mismo que permanece el resto de la temporada, es muy fácil de distinguir ya que son pocas hojas

de tamaño reducido, las cuales incluso podrían confundirse con brácteas. Cuando el follaje del resto de la temporada completa su expansión estas primeras hojas, ya endurecidas mantienen su tamaño reducido. Este follaje incipiente durante la floración coincide con el pico de herbívoros de la región y presentó el mayor porcentaje de daño (30 ± 9%). Lo cual explica su relación positiva con el daño acumulado de 2016 ya que hojas muy jóvenes son más atractivas para los herbívoros pese a ser las más defendidas (Bazzaz *et al.* 1987), así es posible que las plantas más dañadas del 2016 tuvieron menos oportunidades de almacenar recursos generando defensas bajas en este follaje de la floración.

Al contrario de lo esperado, la herbivoría foliar ocurrida durante la floración tuvo un impacto positivo de gran magnitud sobre el número de inflorescencias por rama. Probablemente porque los herbívoros consumen los nuevos brotes de la planta, dañando meristemos florales y vegetativos de manera simultánea. Ante esta situación, la planta compensa esta pérdida liberando otros meristemos (es decir: permitiendo que meristemos latentes se diferencien en florales) generando un incremento en la producción total de inflorescencias. No obstante, es necesario un estudio más cuidadoso para ver si este aumento se ve reflejado progenie producida y si es capaz de aligerar los efectos negativos del daño acumulado de 2016 en flores y frutos, así como el daño foliar de la fructificación en infrutescencias, frutos y semillas (Tuomi *et al.* 1994; Wise *et al.* 2008; Buchanan 2015; Nakahara *et al.* 2018; West and Louda 2018).

Efecto sobre frutos e infrutescencias-Las diferencias encontradas en los niveles de daño dependiendo de la etapa fenológica de las plantas, nos indica que flores y frutos dependen de diferentes recursos (Dominguez and Dirzo 1994). En el primer caso es lo acumulado durante toda la temporada anterior, mientras que el segundo son los fotosintatos producidos durante el periodo de maduración de los frutos, división que se ha observado en *E. xavanence,* otra especie proléptica de la región (Dominguez and Dirzo 1994).

Este efecto negativo de la herbivoría ocurrida una vez que el follaje se expandió en su totalidad, ha sido reportado con anterioridad en *C. nitida* y en *E. xavanense* (Dominguez and Dirzo 1994; Boege 2005a). En general hay un efecto negativo de la defoliación en muchas plantas perenes (Stephenson 1980; Koptur *et al.* 1996; Mothershead and Marquis 2000; Gong and Zhang 2014), aunque hay excepciones (Obeso and Grubb 1993; Agrawal 2000). No obstante, los diseños experimentales de la gran mayoría de estos trabajos han utilizado métodos artificiales de defoliación, así como porcentajes preestablecidos. Se ha visto que el efecto en muchos casos es

diferencial entre herbivoría natural y artificial (Baldwin 1990; Tiffin and Inouye 2000; Inouye and Tiffin 2003). En el presente estudio se obtuvieron resultados similares bajo herbivoría natural, e incluso a tasas mucho más bajas que las reportadas anteriormente para *C. nitida* y otras especies prolépticas (Dominguez and Dirzo 1994; Boege 2005a). Por ejemplo ha sido descrito un efecto compensatorio a tasas del 25% en el follaje posterior a la floración en *C. nítida* (Boege 2005a), mientras que en este estudio, sólo se detectó compensación en la etapa de floración, con efectos indirecto disminuidos de compensación en infrutescencias y frutos.

Se ha propuesto que al haber una relación entre la inducción a la floración y la adquisición de recursos para la fructificación, puede generarse una constricción en el ajuste entre número de flores y disponibilidad de recursos, de tal manera que la sobreproducción de flores puede ser la mejor estrategia bajo condiciones impredecibles (Wiens 1984; Dominguez and Dirzo 1994). Invertir en reproducción sobre herbivoría puede permitir mantener las interacciones planta-polinizador y sostener la producción de descendencia (Lucas-Barbosa *et al.* 2016). Además en plantas perenes se ha documentado que invierten una alta cantidad de sus recursos en tejidos periféricos, de atracción (corolas vistosas, vainas coloridas, etc.; Wenk and Falster 2015; Fridley 2017; Wenk *et al.* 2017), más que en una alta cantidad de frutos y semillas, el fruit set tiende a ser bajo (32.7%; Wiens 1984) ya que tienen múltiples eventos reproductivos a lo largo de su vida. En las plantas anuales suele ocurrir lo contrario, altos porcentajes de fruit set (85%), pues sólo hay un evento reproductivo en su ciclo de vida (Wiens 1984).

Efecto sobre gametos masculinos y femeninos- Se encontró una relación negativa entre el daño foliar acumulado del 2016 y el número de granos de polen por flor, las plantas con mayores niveles de herbivoría presentaron 24.08% menos granos que las plantas con poca herbivoría. Esto indica que el daño foliar acumulado de la temporada anterior (2016) tiene un impacto mayor en otros caracteres, como el número de inflorescencias, o granos de polen, y no tanto en el número de flores en antesis.

El número de estudios dónde evalúan los efectos de la defoliación en la función masculina es relativamente reducido, sin embargo se observa una tendencia negativa tanto en plantas de flores unisexuales como *Cucurbita texana* (monoica) o *Silene latifolia* (dioica) (Quesada *et al.* 1995; Litto *et al.* 2015) así como en las pocas hermafroditas que hay registro, tal es el caso de *Raphanus raphinistrum* (Strauss *et al.* 1996; Lehtila 1999). En especies prolépticas, hasta donde sabemos, la literatura al respecto es inexistente. Una reducción en el número de granos de polen producidos,

implica una disminución en la probabilidad de fecundar algún óvulo, asimismo puede afectar en la atracción de polinizadores disminuyendo aún más las posibilidades de entrecruza (Frazee and Marquis 1994; Quesada *et al.* 1995; Strauss *et al.* 1996, 2001; Lehtila 1999).

Siguiendo el eje temporal, el daño foliar ocurrido durante la floración, al contrario de lo obtenido en el primer análisis, tuvo un impacto negativo de gran magnitud sobre el tamaño del grano de polen, este efecto también se ha observado en algunos estudios (Strauss *et al.* 1996, 2001; Lehtila 1999). Pese a que se sabe que hay cambios en las tasas de herbivoría a lo largo de la temporada (Baldwin 1990; Filip *et al.* 1995), se ha evaluado con menor frecuencia el impacto del cambio, de estas tasas en el éxito reproductivo. No obstante se ha visto que el efecto es diferencial según la temporada en que ocurra la defoliación (García and Ehrlén 2002). Cabe resaltar que generalmente se ha evaluado una tasa de herbivoría puntual que se relaciona, ya sea con el número de granos de polen y/o con el tamaño de los mismos, o bien el cambio temporal se relaciona con otros aspectos como la resistencia o capacidad compensatoria. En este estudio se encontró que el impacto en los caracteres femeninos y masculinos varía según la temporada en que ocurra la herbivoría.

Este hecho permite suponer que el desarrollo y aprovisionamiento de los granos de polen está influido por los primeros fotosintatos de la temporada. En algunos casos se ha observado que la hoja más cercana a las flores tiene un impacto importante en el desarrollo y aprovisionamiento de las mismas (Quesada *et al.* 1995). En cuyo caso es posible que este primer follaje pueda ser importante para el tapetum dado que provee los recursos necesarios para el aprovisionamiento de los granos de polen, mientras que la mayor cantidad de recursos para la producción de las estructuras reproductoras provienen de lo almacenado la temporada anterior. Del mismo modo en estudios dónde han comparado simultáneamente el impacto en la adecuación femenina y en la masculina, esta última tiende a verse más afectada (Lehtila 1999; Litto *et al.* 2015).

Es interesante resaltar que el número de óvulos no se vio afectado directamente por el daño de los herbívoros, únicamente de manera indirecta por el efecto del daño foliar acumulado del 2016 sobre las flores y probablemente inflorescencias. Si tomamos en cuenta el efecto sobre éstas del primer análisis, esto indicaría que hay un reservorio de recursos asignado a la producción y aprovisionamiento de los gametos femeninos. Esta situación se ha observado en especies como *Raphanus raphinistrum*, dónde el número y tamaño de óvulos no se ve afectado por la herbivoría foliar (Lehtila 1999), así mismo en especies monoicas y dioicas las flores femeninas se ven poco o nada afectadas (Narbona and Dirzo 2010; Litto *et al.* 2015), no obstante hay casos aislados como

Chamaecrista fasiculata dónde hay una disminución en el tamaño y número de óvulos, sin embargo, detectaron un impacto mayor de la herbivoría en otros aspectos como la altura, por lo que suponen que los caracteres florales están amortiguados contra la variabilidad en la disponibilidad de recursos (Frazee and Marquis 1994).

Efecto sobre frutos y semillas- En el caso de la herbivoría foliar ocurrida durante la fructificación, se observó un fuerte impacto negativo sobre el número de semillas por fruto. En estudios previos se ha reportado un efecto negativo de la defoliación sobre el número de frutos y/o semillas así como en la masa de las mismas (Stephenson 1980; Dominguez and Dirzo 1994; Niesenbaum 1996; García and Ehrlén 2002; Lehndal *et al.* 2016). En este caso, ambos análisis mostraron un efecto negativo de la defoliación en infrutescencias, frutos y semillas, de tal manera es posible decir que la producción de semillas y aprovisionamiento del embrión, al igual que frutos e infrutescencias, dependen de los fotosintatos producidos durante la temporada, concordando con lo registrado para *E. xavanense* (Dominguez and Dirzo 1994). Muchas plantas perenes invierten gran parte de su esfuerzo reproductivo en estructuras de atracción, más que en la producción de semillas por ciclo reproductivo, ya que poseen múltiples eventos reproductivos (Wenk and Falster 2015; Wenk *et al.* 2017). De tal manera podemos ver que los patrones temporales de distribución de recursos en la planta tienen una influencia en la progenie producida, donde la herbivoría es capaz de interferir (Bazzaz *et al.* 1987; Lucas-barbosa 2016).

El daño foliar acumulado de 2016 presentó de manera indirecta un efecto positivo en el número de semillas mediante la siguiente ruta: El daño foliar acumulado de 2016 tuvo una influencia negativa en el número de granos de polen y estos a su vez se relacionan negativamente con el número de semillas. De tal modo, aquellas plantas que produjeron un mayor número de granos de polen por flor, presentaron un menor número de semillas por fruto, y viceversa. Esto puede indicar que ciertos individuos invierten una mayor cantidad de recursos vía masculina mientras que otros lo hacen vía femenina. Aspecto que se ha planteado en especies como *Raphanus raphinistrum*, donde las plantas más dañadas produjeron más flores (por lo tanto más anteras y granos de polen) pero no más semillas (Strauss *et al.* 2001). Incluso se ha propuesto que la herbivoría podría ser una fuerza selectiva hacia la dioecia (Mutikainen and Delph 1996; McCall and Irwin 2006; Johnson *et al.* 2015). Para evaluar con mayor precisión esta propuesta, habría que hacer un seguimiento temporal en un plazo mayor, ya que las condiciones ambientales podrían

estar influyendo y enmascarar los patrones observados (Normand 2002; Inouye and Tiffin 2003; Barker *et al.* 2019).

Otros efectos y "missing paths"-El tamaño de la planta (medido en términos de la altura inicial) solamente correlacionó con el número de inflorescencias, de tal manera que las plantas más grandes producen una mayor cantidad de inflorescencias, lo cual está directamente relacionado con la arquitectura de la planta pues de ello depende cuántos meristemos es capaz de activar cada individuo (Lovett-Doust 1989; Boege 2005b). Las relaciones positivas dadas entre inflorescencias, flores, infrutescencias y frutos concuerdan con lo esperado ya que un despliegue floral vistoso atraerá más visitantes y probablemente generará un mayor número de frutos e infrutescencias (Worley and Barrett 2000; Harder and Barrett 2006; Sargent *et al.* 2007).

Como era esperado la sincronía de la floración presentó una fuerte relación positiva con la precipitación. Así mismo se esperaba que correlacionara con la cantidad de frutos producidos, sin embargo, ninguna otra relación propuesta fue significativa. No obstante un "missing path" obtenido arrojó una relación significativa entre la precipitación ocurrida durante la floración y el número de frutos. Posiblemente, esto se deba a alguna variable que no fue contemplada en el presente estudio y cuyo efecto se ve reflejado en esta relación. Es posible que aquellos individuos que florecieron en los días de mayor precipitación, sean capaces de mantener un follaje más hidratado y por lo tanto mantener los recursos necesarios para una mayor cantidad de frutos, dado que el nivel de agua en las hojas cambia a lo largo de la temporada, siendo mayor al inicio (73.2%) disminuyendo hacia el final de la misma (57.9%) (Boege 2005a).

También se encontró una relación negativa entre crecimiento y el número de frutos por rama, es decir, aquellas ramas que se elongaron más, tuvieron menos infrutescencias y viceversa. Esto indica una posible disyuntiva funcional entre los recursos que la planta destina para sostener las infrutescencias, y los destinados para el crecimiento vegetativo. De tal manera, hay un recurso limitante para estos dos caracteres, ya que la reproducción tiene un costo fisiológico, utilizando recursos que se pueden destinar al a crecimiento vegetativo (Bazzaz *et al.* 1987; Calvo 1993; Fridley 2017).

Finalmente se detectaron cuatro "missing paths" en el segundo análisis (caracteres menores; Fig. 4). Sin embargo, los "missing paths" significativos pueden ser incorporados al modelo o ser especificados como errores de correlación entre variables y no formar parte del modelo, es decir

no son considerados causales pero tienen una relación significativa (Bitenc *et al.* 2017). Los análisis muestran que la floración depende en su mayoría de los recursos acumulados durante la temporada anterior, mientras que la fructificación depende de lo producido en la temporada actual, no obstante, esto no implica que el uso de recursos por parte de ambas fuentes estén disociadas y puede suceder que un gasto excesivo en los caracteres florales (diámetro y óvulos), comprometa el aprovisionamiento de los embriones y la defensa posterior.

CONCLUSIONES

Si bien los estudios sobre herbivoría y éxito reproductivo tuvieron un auge durante las décadas de 1980 y 1990, se sigue intentando comprender los alcances de esta relación depredador-planta, así como los factores que contribuyen y modifican el resultado final. En el presente estudio se abordó esta relación tratando de abarcar la mayor variedad posible de componentes de la adecuación, asociados a un eje temporal de herbivoría. Fue posible detectar cambios en los estimados de daño foliar, donde la herbivoría acumulada de 2016 tuvo un extenso impacto, no sólo afectó caracteres reproductivos de la siguiente temporada si no que también afectó los porcentajes de daño foliar durante la floración. De tal manera que tuvo influencia en la mayoría de variables evaluadas ya sea directa o indirectamente. Este tipo de análisis permite visualizar una red de relaciones entre variables, mostrando un panorama más cercano a lo que sucede en la naturaleza. Si bien hay inconvenientes, debido a la falta de control de variables externas, entender la mecánica de la herbivoría a nivel individual, permite un mejor entendimiento de las interacciones y cómo sus efectos van más allá en la dinámica del individuo, de igual modo, estos efectos internos pueden influenciar otras interacciones. Sin embargo, es necesario realizar estudios a largo plazo que incluyan otros factores que pueden estar influenciando, como variables ambientales o polinizadores. Aún hay un amplio campo de estudio en este tema ya que las respuestas varían entre especies y ecosistemas.

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APPENDIX S1

Endogenous variables models and *basis set* models for major and smaller characters path analysis

Models integrating the analysis of major characters: first structural analysis

Folivory$_{16cu}$

```
mod.Foli.2016 <- lmer((Foli.2016) ~ scale(height) + (1|Site), data=datos)

                      Estimate Std. Error t value Chisq Df Pr(>Chisq)
(Intercept)           0.136191   0.007578  17.973
scale(Height)         0.012066   0.007339   1.644 2.7351  1    0.09817
```

Inflorescences

```
mod.inflo <- lme((Inflo) ~ scale(Height) + scale(Foli.2016) + scale(Foli.flo) +
scale(Rainfall), random = ~1|Site, weights = varPower(form = ~fitted(.)), data=datos)

                         Value Std.Error DF   t-value p-value Chisq Df Pr(>Chisq)
(Intercept)          100.10846  25.43013 39  3.936608  0.0003
scale(Height)         28.57484  10.22484 39  2.794649  0.0080 7.8101  1   0.005196 **
scale(Foli.2016)     -32.38194  12.39297 39 -2.612927  0.0127 6.8274  1   0.008977 **
scale(Foli.flo)       29.16454  13.59244 39  2.145644  0.0382 4.6038  1   0.031901 *
scale(Rainfall)       14.42182  11.80266 39  1.221912  0.2291 1.4931  1   0.221741
```

Flowers

```
mod.Flo <- glmer(Flo ~ (scale(Inflo) + scale(Rainfall) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo)) + (1|Site) + (1|id), family="poisson", data = datos)

                      Estimate Std. Error z value Pr(>|z|)     Chisq Df Pr(>Chisq)
(Intercept)            3.59482    0.13089  27.465  < 2e-16 ***
scale(Inflo)           0.48810    0.13676   3.569 0.000358 *** 12.7383  1  0.0003583 ***
scale(Rainfall)        0.01979    0.13526   0.146 0.883673     0.0214  1  0.8836729
scale(Height)         -0.07311    0.13936  -0.525 0.599869     0.2752  1  0.5998689
scale(Foli.2016)      -0.41133    0.14718  -2.795 0.005195 **  7.8104  1  0.0051947 **
scale(Foli.flo)       -0.06711    0.13986  -0.480 0.631345     0.2302  1  0.6313449
```

Folivory$_{flo}$

```
mod.Foli.flo <- lmer((Foli.flo) ~ scale(Height) + scale(Foli.2016) + (1|Site), data=datos)

                      Estimate Std. Error t value Chisq Df Pr(>Chisq)
(Intercept)            0.31201    0.03520   8.863
scale(Height)         -0.01688    0.01260  -1.340 1.8362  1    0.17540
scale(Foli.2016)       0.03066    0.01247   2.459 6.2999  1    0.01207 *
```

Folivory$_{fru}$

```
mod.Foli.fru <- lmer((Foli.fru) ~ scale(Height) + scale(Foli.flo) + (1|Site), data=datos)

                       Estimate Std. Error t value Chisq Df Pr(>Chisq)
(Intercept)            0.115718   0.005516  20.978
scale(Height)         -0.001883   0.005590  -0.337 0.1214  1     0.7276
scale(Foli.flo)        0.008237   0.005590   1.473 2.3226  1     0.1275
```

Infructescences

```
zctmod.infru<- glmmTMB(Infru ~ scale(Height) + scale(Foli.fru) + scale(Inflo) + (Synchrony)
+ (1 | Site), ziformula = ~ 1, data = datos, family = poisson)
zctmod.infru.nb <- update(zctmod.infru,family=nbinom2)

                      Estimate Std. Error z value Pr(>|z|)
(Intercept)            1.02644    0.31389   3.270  0.00108 **
scale(Height)          0.07956    0.26184   0.304  0.76124
scale(Foli.fru)       -0.60331    0.25529  -2.363  0.01812 *
scale(Inflo)           1.07618    0.34194   3.147  0.00165 **
scale(Synchrony)      -0.06977    0.35553  -0.196  0.84442
```

```
#### Fruits ####
zctmod.fru<- glmmTMB((Fru) ~ scale(Flo) + scale(Infru) + scale(Foli.fru) + scale(Height) +
scale(Synchrony) + (1 | Site), ziformula = ~ 1, data = datos, family = poisson)

                     Estimate Std. Error z value Pr(>|z|)
(Intercept)           0.42176    0.20842   2.024  0.04301 *
scale(Flo)            0.34683    0.13317   2.604  0.00920 **
scale(Infru)          0.18979    0.05153   3.683  0.00023 ***
scale(Foli.fru)      -0.49587    0.17613  -2.815  0.00487 **
scale(Height)        -0.11592    0.14731  -0.787  0.43134
scale(Synchrony)      0.07781    0.13113   0.593  0.55294

#### Vegetative growth ####
mod.grw <- lmer((Veg.growth) ~ scale(Height) + scale(Foli.fru) + scale(Foli.2016) +
scale(Flo) + scale(Fru) + (1|Site), data=datos)

                     Estimate Std. Error t value Chisq Df Pr(>Chisq)
(Intercept)            9.7669     0.5635  17.331
scale(Height)         -0.6073     0.5642  -1.076 1.2774  1     0.2584
scale(Foli.fru)       -0.8774     0.5977  -1.468 2.4421  1     0.1181
scale(Foli.2016)      -0.1151     0.6699  -0.172 0.0371  1     0.8473
scale(Flo)             0.4066     0.8008   0.508 0.3485  1     0.5550
scale(Fru)            -0.1824     0.7387  -0.247 0.0970  1     0.7554


#### Synchrony ####
mod.sync <- lmer(Synchrony ~ scale(Rainfall) + (1|Site), data=datos)

                     Estimate Std. Error t value Chisq Df Pr(>Chisq)
(Intercept)           216.435      7.698   28.12
scale(Rainfall)        87.874      7.783   11.29 127.48  1  < 2.2e-16 ***
```

Significant missing Paths

```
### Condition 6 ####
mod.cond6<- glmmTMB((Fru) ~ scale(Rainfall) + scale(Synchrony) + scale(Height) +
scale(Foli.fru) + scale(Infru) + scale(Flo) + (1 | Site), ziformula = ~scale(Flo) , data =
datos, family = poisson)
mod.cond6.null<- glmmTMB((Fru) ~ scale(Synchrony) + scale(Height) + scale(Foli.fru) + scale(Infru) +
scale(Flo) + (1 | Site), ziformula = ~scale(Flo) , data = datos, family = poisson)

                     Estimate Std. Error z value Pr(>|z|)
(Intercept)           0.28392    0.26950   1.053 0.292115
scale(Rainfall)       0.97032    0.37234   2.606 0.009161 **
scale(Synchrony)     -0.92326    0.38243  -2.414 0.015769 *
scale(Height)        -0.07989    0.14969  -0.534 0.593550
scale(Foli.fru)      -0.56851    0.16684  -3.407 0.000656 ***
scale(Infru)          0.11497    0.06556   1.754 0.079491 .
scale(Flo)            0.44959    0.15453   2.909 0.003621 **

              Df    AIC    BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond6.null  9 148.08 164.54 -65.04   130.08
mod.cond6      10 143.18 161.47 -61.59   123.18 6.8998      1   0.008621 **

### Condition 26 ####
mod.cond26 <- lmer(Veg.growth ~ scale(Infru) + scale(Synchrony) + scale(Height) +
scale(Foli.fru) + scale(Inflo) + scale(Foli.2016) + scale(Flo) + scale(Fru) + (1|Site),
data=datos)
mod.cond26.null <- lmer(Veg.growth ~ scale(Synchrony) + scale(Height) + scale(Foli.fru) + scale(Inflo) +
scale(Foli.2016) + scale(Flo) + scale(Fru) + (1|Site), data=datos)

                     Estimate Std. Error t value Chisq Df Pr(>Chisq)
(Intercept)            9.7087     0.6582  14.751
scale(Infru)          -2.7786     0.7918  -3.509 12.3144  1  0.0004495 ***
scale(Synchrony)       0.2288     0.5143   0.445  0.1979  1  0.6564282
scale(Height)         -0.4166     0.5138  -0.811  0.6574  1  0.4174836
scale(Foli.fru)       -0.7643     0.5397  -1.416  2.0056  1  0.1567239
scale(Inflo)          -0.5907     0.6355  -0.929  0.8639  1  0.3526359
scale(Foli.2016)       0.1043     0.6062   0.172  0.0296  1  0.8633723
scale(Flo)             0.6386     0.8519   0.750  0.5619  1  0.4535000
```

```
scale(Fru)               2.2300     0.9416   2.368  5.6089  1  0.0178699 *
                Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond26.null 10 261.69 279.98 -120.84   241.69
mod.cond26      11 250.95 271.06 -114.47   228.95 12.741      1  0.0003578 ***
```

Models integrating the major characters analysis *basis set*

```
mod.cond1 <- lmer( Height ~ scale(Rainfall)  + (1|Site), data=datos)
mod.cond1.null <- lmer(Height ~ 1 + (1|Site), data=datos)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond1.null  3 573.49 578.98 -283.75   567.49
mod.cond1       4 575.37 582.68 -283.68   567.37 0.1251      1     0.7236

mod.cond2 <- lmer(Foli.2016 ~ scale(Rainfall) + scale(Height) + (1|Site), data=datos)
mod.cond2.null <- lmer(Foli.2016 ~ scale(Height) + (1|Site), data=datos)

               Df     AIC     BIC logLik deviance Chisq Chi Df Pr(>Chisq)
mod.cond2.null  4 -140.55 -133.24 74.275  -148.55
mod.cond2       5 -139.07 -129.93 74.536  -149.07 0.521      1     0.4704

mod.cond3 <- lmer(Foli.flo ~ scale(Rainfall) + scale(Height) + scale(Foli.2016) + (1|Site),
data=datos)
mod.cond3.null <- lmer(Foli.flo ~ scale(Height) + scale(Foli.2016) + (1|Site), data=datos)

               Df     AIC     BIC logLik  deviance  Chisq Chi Df Pr(>Chisq)
mod.cond3.null  5 -89.001 -79.858 49.501  -99.001
mod.cond3       6 -89.590 -78.618 50.795 -101.590 2.5883      1     0.1077

mod.cond4 <- lmer(Foli.fru ~ scale(Rainfall) + scale(Height) + scale(Foli.flo) + (1|Site),
data=datos)
mod.cond4.null <- lmer(Foli.fru ~ scale(Height) + scale(Foli.flo) + (1|Site), data=datos)

               Df     AIC     BIC logLik  deviance  Chisq Chi Df Pr(>Chisq)
mod.cond4.null  5 -164.85 -155.71 87.424  -174.85
mod.cond4       6 -162.93 -151.96 87.465  -174.93 0.0807      1     0.7763

mod.cond5<- glmmTMB(Infru ~ scale(Rainfall) + scale(Synchrony) + scale(Height) +
scale(Foli.fru) + scale(Inflo) + (1 | Site), ziformula = ~ 1, data = datos, family =
poisson)
mod.cond5nb2 <- update(mod.cond5,family=nbinom2)
mod.cond5.null<- glmmTMB(Infru ~ scale(Synchrony) + scale(Height) + scale(Foli.fru) +
scale(Inflo) + (1 | Site), ziformula = ~ 1, data = datos, family = poisson)
mod.cond5nb2.null <- update(mod.cond5.null,family=nbinom2)

                  Df    AIC    BIC  logLik deviance Chisq Chi Df Pr(>Chisq)
mod.cond5nb2.null  8 222.26 236.89 -103.13   206.26
mod.cond5.nb2      9 220.48 236.94 -101.24   202.48 3.783      1    0.05178 .

mod.cond6<- glmmTMB((Fru) ~ scale(Rainfall) + scale(Synchrony) + scale(Height) +
scale(Foli.fru) + scale(Infru) + scale(Flo) + (1 | Site), ziformula = ~scale(Flo) , data =
datos, family = poisson)
mod.cond6.null<- glmmTMB((Fru) ~ scale(Synchrony) + scale(Height) + scale(Foli.fru) +
scale(Infru) + scale(Flo) + (1 | Site), ziformula = ~scale(Flo) , data = datos, family =
poisson)

               Df    AIC    BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond6.null  9 148.08 164.54 -65.04   130.08
mod.cond6      10 143.18 161.47 -61.59   123.18 6.8998      1   0.008621 **

mod.cond7 <- lmer(Veg.growth ~ scale(Rainfall) + scale(Height) + scale(Foli.2016) +
scale(Foli.fru) + scale(Flo) + scale(Fru) + (1|Site), data=datos)
mod.cond7.null <- lmer(Veg.growth ~ scale(Height) + scale(Foli.2016) + scale(Foli.fru) +
scale(Flo) + scale(Fru) + (1|Site), data=datos)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond7.null  8 258.86 273.49 -121.43   242.86
mod.cond7       9 260.74 277.20 -121.37   242.74 0.1216      1     0.7273
```

```
mod.cond8 <- lmer(Height ~ scale(Synchrony) + scale(Rainfall) + (1|Site), data=datos)
mod.cond8.null <- lmer(Height ~ scale(Rainfall) + (1|Site), data=datos)

              Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond8.null  4 575.37 582.68 -283.68   567.37
mod.cond8       5 576.84 585.98 -283.42   566.84 0.5286      1     0.4672

mod.cond9 <- lmer(Foli.2016 ~ scale(Synchrony) + scale(Rainfall) + scale(Height) +
(1|Site), data=datos)
mod.cond9.null <- lmer(Foli.2016 ~ scale(Rainfall) + scale(Height) + (1|Site), data=datos)

              Df     AIC     BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond9.null  5 -139.07 -129.93 74.536  -149.07
mod.cond9       6 -137.08 -126.11 74.539  -149.08 0.0076      1     0.9307

mod.cond10 <- lmer(Foli.flo ~ scale(Synchrony) + scale(Rainfall) + scale(Height) +
scale(Foli.2016) + (1|Site), data=datos)
mod.cond10.null <- lmer(Foli.flo ~ scale(Rainfall) + scale(Height) +
scale(Foli.2016) + (1|Site), data=datos)

               Df     AIC     BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond10.null  6 -89.590 -78.618 50.795  -101.59
mod.cond10       7 -89.322 -76.521 51.661  -103.32 1.7317      1     0.1882

mod.cond11 <- lmer(Foli.fru ~ scale(Synchrony) + scale(Rainfall) + scale(Height) +
scale(Foli.flo) + (1|Site), data=datos)
mod.cond11.null <- lmer(Foli.fru ~ scale(Rainfall) + scale(Height) + scale(Foli.flo) +
(1|Site), data=datos)

               Df     AIC     BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond11.null  6 -162.93 -151.96 87.465  -174.93
mod.cond11       7 -161.59 -148.79 87.794  -175.59 0.6587      1      0.417

mod.cond12 <- glmer(Inflo ~ (scale(Synchrony) + scale(Rainfall) + scale(Height) +
scale(Foli.2016) + scale(Foli.flo)) + (1|Site) +  (1|id), family="poisson", data = datos)
mod.cond12.null <- glmer(Inflo ~ (scale(Rainfall) + scale(Height)
+ scale(Foli.2016) + scale(Foli.flo)) + (1|Site) +  (1|id), family="poisson", data = datos)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond12.null  7 533.37 546.17 -259.68   519.37
mod.cond12       8 535.36 549.99 -259.68   519.36 0.0063      1     0.9369

mod.cond13 <- glmer(Flo ~ (scale(Synchrony) + scale(Rainfall) + scale(Height) +
scale(Foli.2016) + scale(Foli.flo) + scale(Inflo)) + (1|Site) +  (1|id), family="poisson",
data = datos)
mod.cond13.null <- glmer(Flo ~ (scale(Rainfall) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + scale(Inflo)) + (1|Site) +  (1|id), family="poisson", data = datos)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond13.null  8 467.34 481.97 -225.67   451.34
mod.cond13       9 466.35 482.81 -224.18   448.35 2.9872      1    0.08392 .

mod.cond14 <- lmer(Veg.growth ~ scale(Synchrony) + scale(Rainfall) + scale(Height) +
scale(Foli.2016) + scale(Foli.fru) + scale(Flo) + scale(Fru) + (1|Site), data=datos)
mod.cond14.null <- lmer(Veg.growth ~ scale(Rainfall) + scale(Height)
+ scale(Foli.2016) + scale(Foli.fru) + scale(Flo) + scale(Fru) + (1|Site), data=datos)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond14.null  9 260.74 277.20 -121.37   242.74
mod.cond14      10 262.73 281.01 -121.36   242.73 0.0115      1     0.9147

mod.cond15 <- lmer(Foli.fru ~ scale(Foli.2016) + scale(Height) + scale(Foli.flo) +
(1|Site), data=datos)
mod.cond15.null <- lmer(Foli.fru ~ scale(Height) + scale(Foli.flo) + (1|Site), data=datos)

               Df     AIC     BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond15.null  5 -164.85 -155.71 87.424  -174.85
mod.cond15       6 -164.34 -153.36 88.168  -176.34 1.4867      1     0.2227
```

```
mod.cond16<- glmmTMB(Infru ~ scale(Foli.2016) + scale(Height) + scale(Synchrony) +
scale(Foli.fru) + scale(Inflo) + (1 | Site), ziformula = ~ 1, data = datos, family =
poisson)
mod.cond16.nb2 <- update(mod.cond16,family=nbinom2)
mod.cond16.null <- glmmTMB(Infru ~ scale(Height) + scale(Synchrony) + scale(Foli.fru) +
scale(Inflo) + (1 | Site), ziformula = ~ 1, data = datos, family = poisson)
mod.cond16nb2.null <- update(mod.cond16,family=nbinom2)

                  Df    AIC    BIC  logLik deviance Chisq Chi Df Pr(>Chisq)
mod.cond16.nb2     9 222.53 238.99 -102.27   204.53
mod.cond16nb2.null  9 222.53 238.99 -102.27   204.53     0      0          1

mod.cond17<- glmmTMB((Fru) ~ scale(Foli.2016) + scale(Height) + scale(Synchrony) +
scale(Foli.fru) + scale(Infru) + scale(Flo) + (1 | Site), ziformula = ~scale(Flo) , data =
datos, family = poisson)
mod.cond17.null<- glmmTMB((Fru) ~ scale(Height) + scale(Synchrony) + scale(Foli.fru) +
scale(Infru) + scale(Flo) + (1 | Site), ziformula = ~scale(Flo) , data = datos, family =
poisson)

                Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond17.null  9 148.08 164.54 -65.040   130.08
mod.cond17      10 148.68 166.97 -64.341   128.68 1.3974      1     0.2372

mod.cond18<- glmmTMB(Infru ~ scale(Foli.flo) + scale(Height) + scale(Foli.2016) +
scale(Synchrony) + scale(Foli.fru) + scale(Inflo) + (1 | Site), ziformula = ~ 1, data =
datos, family = poisson)
mod.cond18.null<- glmmTMB(Infru ~ scale(Height) + scale(Foli.2016) + scale(Synchrony) +
scale(Foli.fru) + scale(Inflo) + (1 | Site), ziformula = ~ 1, data = datos, family =
poisson)

                  Df    AIC    BIC  logLik deviance Chisq Chi Df Pr(>Chisq)
mod.cond18.nb2     10 224.42 242.71 -102.21   204.42
mod.cond18nb2.null 10 224.42 242.71 -102.21   204.42     0      0          1

mod.cond19<- glmmTMB((Fru) ~ scale(Foli.flo) + scale(Height) + scale(Foli.2016) +
scale(Synchrony) + scale(Foli.fru) + scale(Infru) + scale(Flo) + (1 | Site), ziformula =
~scale(Flo) , data = datos, family = poisson)
mod.cond19.null<- glmmTMB((Fru) ~ scale(Height) + scale(Foli.2016) + scale(Synchrony) +
scale(Foli.fru) + scale(Infru) + scale(Flo) + (1 | Site), ziformula = ~scale(Flo) , data =
datos, family = poisson)

                Df    AIC    BIC  logLik deviance Chisq Chi Df Pr(>Chisq)
mod.cond19.null 10 148.68 166.97 -64.341   128.68
mod.cond19      11 148.09 168.21 -63.046   126.09  2.59      1     0.1075

mod.cond20 <- lmer(Veg.growth ~ scale(Foli.flo) + scale(Height) + scale(Foli.2016) +
scale(Foli.fru) + scale(Flo) + scale(Fru) + (1|Site), data=datos)
mod.cond20.null <- lmer(Veg.growth ~ scale(Height) + scale(Foli.2016) + scale(Foli.fru) +
scale(Flo) + scale(Fru) + (1|Site), data=datos)

                Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond20.null  8 258.86 273.49 -121.43   242.86
mod.cond20       9 259.66 276.12 -120.83   241.66 1.2007      1     0.2732

mod.cond21 <- glmer(Inflo ~ (scale(Foli.fru) + scale(Height) + scale(Foli.flo) +
scale(Rainfall) + scale(Foli.2016)) + (1|Site) +  (1|id), family="poisson", data = datos)
mod.cond21.null <- glmer(Inflo ~ (scale(Height) + scale(Foli.flo) + scale(Rainfall) +
scale(Foli.2016)) + (1|Site) +  (1|id), family="poisson", data = datos)

                Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond21.null  7 533.37 546.17 -259.68   519.37
mod.cond21       8 533.10 547.73 -258.55   517.10 2.2673      1     0.1321

mod.cond22 <- glmer(Flo ~ (scale(Foli.fru) + scale(Height) + scale(Foli.flo) +
scale(Rainfall) + scale(Foli.2016) + scale(Inflo)) + (1|Site) +  (1|id), family="poisson",
data = datos)
mod.cond22.null <- glmer(Flo ~ (scale(Height) + scale(Foli.flo) + scale(Rainfall) +
scale(Foli.2016) + scale(Inflo)) + (1|Site) +  (1|id), family="poisson", data = datos)

                Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
```

```
mod.cond22.null  8 467.34 481.97 -225.67   451.34
mod.cond22       9 469.31 485.77 -225.66   451.31 0.0273      1     0.8687
```

```
mod.cond23<- glmmTMB((Fru) ~ scale(Inflo) + scale(Rainfall) + scale(Height) +
scale(Foli.2016) + scale(Foli.flo) + scale(Synchrony) + scale(Foli.fru) + scale(Infru) +
scale(Flo) + (1 | Site), ziformula = ~scale(Flo) , data = datos, family = poisson)
mod.cond23.null <- glmmTMB((Fru) ~ scale(Rainfall) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + scale(Synchrony) + scale(Foli.fru) + scale(Infru) + scale(Flo) + (1 |
Site), ziformula = ~scale(Flo) , data = datos, family = poisson)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond23.null 12 142.90 164.84 -59.450   118.90
mod.cond23      13 144.55 168.32 -59.273   118.55 0.3537      1      0.552
```

```
mod.cond24 <- lmer(Veg.growth ~ scale(Inflo) + scale(Rainfall) + scale(Height) +
scale(Foli.2016) + scale(Foli.flo) + scale(Foli.fru) + scale(Flo) + scale(Fru) + (1|Site),
data=datos)
mod.cond24.null <- lmer(Veg.growth ~ scale(Rainfall) + scale(Height)
+ scale(Foli.2016) + scale(Foli.flo) + scale(Foli.fru) + scale(Flo) + scale(Fru) +
(1|Site), data=datos)
               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond24.null 10 261.52 279.81 -120.76   241.52
mod.cond24      11 262.74 282.86 -120.37   240.74 0.7808      1     0.3769
```

```
mod.cond25 <- glmer.nb(Flo ~ scale(Infru) + scale(Synchrony) + scale(Height) +
scale(Foli.fru) + scale(Inflo) + scale(Rainfall)
+ scale(Foli.2016) + scale(Foli.flo) + (1 | Site), data = datos)
mod.cond25.null <- glmer.nb(Flo ~ scale(Synchrony) + scale(Height)
+ scale(Foli.fru) + scale(Inflo) + scale(Rainfall) + scale(Foli.2016) + scale(Foli.flo) +
(1 | Site), data = datos)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond25.null 10 463.87 482.15 -221.93   443.87
mod.cond25      11 463.95 484.07 -220.98   441.95 1.9157      1     0.1663
```

```
mod.cond26 <- lmer(Veg.growth ~ scale(Infru) + scale(Synchrony) + scale(Height) +
scale(Foli.fru) + scale(Inflo) + scale(Foli.2016) + scale(Flo) + scale(Fru) + (1|Site),
data=datos)
mod.cond26.null <- lmer(Veg.growth ~ scale(Synchrony) + scale(Height) + scale(Foli.fru) +
scale(Inflo) + scale(Foli.2016) + scale(Flo) + scale(Fru) + (1|Site), data=datos)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond26.null 10 261.69 279.98 -120.84   241.69
mod.cond26      11 250.95 271.06 -114.47   228.95 12.741      1  0.0003578 ***
```

Models integrating the Analysis of smaller characters: Second structural analysis

```
#### Flowers ####
mod.flo <- glmer.nb((Flo) ~ scale(Foli.2016) + scale(Foli.flo) + scale(Height) + (1|Site),
data=datos)

               Estimate Std. Error z value Pr(>|z|)  Chisq    Df Pr(>Chisq)
(Intercept)      4.1432     0.1246  33.243  < 2e-16
scale(Foli.2016) -0.3894     0.1181  -3.299 0.000971 10.8829  1  0.0009705 ***
scale(Foli.flo)  -0.2422     0.1435  -1.687 0.091567  2.8464  1  0.0915814
scale(Height)    -0.1272     0.1316  -0.967 0.333759  0.9341  1  0.3337918
```

```
#### Fruits ####
zctmod.fru <- glmmTMB((Fru) ~ scale(Foli.fru) + scale(PG.num) + scale(Flo) + scale(FD) +
scale(Height) + (1 | Site), ziformula  = ~ 1, data = datos, family = poisson)

                  Estimate Std. Error z value Pr(>|z|)
(Intercept)        -0.04689    0.45060  -0.104 0.917123
scale(Foli.fru)    -0.06071    0.31477  -0.193 0.847065
scale(PG.num)      -0.05092    0.20286  -0.251 0.801815
scale(Flo)          0.58024    0.20838   2.785 0.005361 **
scale(FD)           1.00864    0.29978   3.365 0.000767 ***
scale(Height)       0.09201    0.24579   0.374 0.708142
```

Floral diameter

```
mod.diam <- lme((FD) ~ scale(Foli.2016) + scale(Foli.flo) + scale(Flo) + scale(Height),
random= ~1|Site, data=datos, weights=varIdent(form = ~ 1 | Site),
control=list(maxIter=500))
```

	Value	Std.Error	DF	t-value	p-value	Chisq	Df	Pr(>Chisq)
(Intercept)	7.474736	0.1833733	23	40.76240	0.0000			
scale(Foli.2016)	0.002244	0.1590437	23	0.01411	0.9889	0.0002	1	0.9887
scale(Foli.flo)	-0.012938	0.1325805	23	-0.09759	0.9231	0.0095	1	0.9223
scale(Flo)	0.135223	0.1462998	23	0.92429	0.3649	0.8543	1	0.3553
scale(Height)	0.048955	0.1092858	23	0.44796	0.6584	0.2007	1	0.6542

Ovule number

```
mod.ov <- lmer(Ov.num ~ scale(Foli.2016) + scale(Foli.flo) + scale(PG.num) + scale(Height)
+ (1|Site), data=datos)
```

	Estimate	Std. Error	t value	Chisq	Df	Pr(>Chisq)
(Intercept)	22.6433	0.7402	30.590			
scale(Foli.2016)	-1.1803	0.8118	-1.454	2.1139	1	0.1460
scale(Foli.flo)	0.2617	0.8014	0.327	0.1066	1	0.7440
scale(PG.num)	0.7434	0.8080	0.920	0.8467	1	0.3575
scale(Height)	0.2968	0.7870	0.377	0.1422	1	0.7061

Pollen grain size

```
mod.pgz <- lmer(PG.siz ~ scale(Foli.2016) + scale(Foli.flo) + scale(Height) + (1|Site),
data=datos)
```

	Estimate	Std. Error	t value	Chisq	Df	Pr(>Chisq)
(Intercept)	26.2657	0.6499	40.416			
scale(Foli.2016)	0.5162	0.5351	0.965	0.9304	1	0.33477
scale(Foli.flo)	-1.1448	0.5340	-2.144	4.5965	1	0.03204 *
scale(Height)	-0.1857	0.5297	-0.351	0.1229	1	0.72587

Pollen grain number

```
mod.pgn <- lme((PG.num) ~ scale(Foli.2016) + scale(Foli.flo) + scale(Height), weights =
varPower(form = ~fitted(.)), random = ~1|Site,data=datos)
```

	Value	Std.Error	DF	t-value	p-value	Chisq	Df	Pr(>Chisq)
(Intercept)	809.3284	60.35444	24	13.409593	0.0000			
scale(Foli.2016)	-146.4996	53.67487	24	-2.729389	0.0117	7.4496	1	0.006345 **
scale(Foli.flo)	0.1229	44.99322	24	0.002731	0.9978	0.0000	1	0.997821
scale(Height)	51.7401	53.51994	24	0.966744	0.3433	0.9346	1	0.333672

Seeds

```
zctmod.seed <- glmmTMB(No.Sem ~ scale(Foli.fru) + scale(PG.num) + scale(Ov.num) +
scale(Height) + (1 | Site), ziformula = ~ 1, data = datos, family = gaussian)
```

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.41157	0.26429	5.341	9.24e-08 ***
scale(Foli.fru)	-0.50473	0.20115	-2.509	0.01210 *
scale(PG.num)	-0.46846	0.15533	-3.016	0.00256 **
scale(Ov.num)	-0.06368	0.17336	-0.367	0.71336
scale(Height)	-0.30625	0.16926	-1.809	0.07041 .

Folivory$_{flo}$

```
mod.foli.flo <- lmer((Foli.flo) ~ scale(Foli.2016) + scale (Height) + (1|Site), data=datos)
```

	Estimate	Std. Error	t value	Chisq	Df	Pr(>Chisq)
(Intercept)	0.33260	0.04362	7.625			
scale(Foli.2016)	0.03396	0.01578	2.152	4.8077	1	0.02833 *
scale(Height)	-0.02171	0.01656	-1.311	1.7375	1	0.18746

Folivory$_{16cu}$

```
mod.foli.16 <- lmer((Foli.2016) ~ scale(Height) + (1|Site), data=datos)
```

	Estimate	Std. Error	t value	Chisq	Df	Pr(>Chisq)
(Intercept)	0.132482	0.011594	11.427			
scale(Height)	0.014146	0.009446	1.497	1.7334	1	0.188

Folivory$_{fru}$

```
mod.foli.fru <- lmer((Foli.fru) ~ scale(Height) + scale(Foli.flo) + (1|Site), data=datos)

             Estimate Std. Error t value    Chisq Df Pr(>Chisq)
(Intercept)    0.075698   0.024880   3.043
scale(Height) -0.005034   0.007173  -0.702  0.5472  1    0.45946
Scale(Foli.flo)0.011235   0.007173   1.566  2.7261  1    0.09872
```

Significant missing Paths

```
### Condition 14 ###
mod.cond14 <- lmer(Foli.fru ~ scale(Ov.num) + scale(Height) + scale(Foli.2016) +
                     scale(Foli.flo) + scale(PG.num) + (1|Site), data=datos)

                 Estimate Std. Error t value   Chisq Df Pr(>Chisq)
(Intercept)       0.113073   0.006906  16.374
scale(Ov.num)    -0.014264   0.007517  -1.898 3.6006  1    0.05776 .
scale(Height)    -0.005275   0.007364  -0.716 0.5131  1    0.47378
scale(Foli.2016) -0.002436   0.007888  -0.309 0.0954  1    0.75746
scale(Foli.flo)   0.010438   0.007492   1.393 1.9407  1    0.16359
scale(PG.num)    -0.002062   0.007664  -0.269 0.0724  1    0.78788

                Df      AIC     BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond14.null  7  -99.852 -90.044 56.926  -113.85
mod.cond14       8 -102.046 -90.836 59.023  -118.05 4.1935      1    0.04058 *

### condition 16 ###
mod.cond16 <- lme((Foli.fru) ~ scale(FD) + scale(Height)+ scale(Foli.2016) +
scale(Foli.flo) + scale(Flo), random= ~1|Site, data=datos, method = "ML",
weights=varIdent(form = ~ 1 | Site), control=list(maxIter=500))

                       Value   Std.Error DF   t-value p-value Chisq Df Pr(>Chisq)
(Intercept)          0.10707471 0.004964950 22 21.566123  0.0000
scale(FD)           -0.01530647 0.005267263 22 -2.905962  0.0082 10.5558  1   0.001158 **
scale(Height)       -0.00600391 0.005062355 22 -1.185991  0.2483  1.7582  1   0.184847
scale(Foli.2016)     0.00331672 0.006512328 22  0.509298  0.6156  0.3242  1   0.569076
scale(Foli.flo)      0.00815125 0.004612705 22  1.767130  0.0911  3.9034  1   0.048187 *
scale(Flo)          -0.00451590 0.006173233 22 -0.731530  0.4722  0.6689  1   0.413429

               Model df       AIC        BIC   logLik   Test  L.Ratio p-value
mod.cond16          1 10 -110.5579  -96.54589 65.27893
mod.cond16.null     2  9 -118.4400 -105.82918 68.21998 1 vs 2 5.882096  0.0153

### Condition 19 ###
mod.cond19 <- lmer((Ov.num) ~ scale(Flo) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + scale(PG.num) + (1|Site), data=datos)

                 Estimate Std. Error t value  Chisq Df Pr(>Chisq)
(Intercept)       22.6433     0.6403  35.361
scale(Flo)         2.6225     0.8551   3.067  9.4058  1   0.002163 **
scale(Height)      0.4898     0.6838   0.716  0.5132  1   0.473772
scale(Foli.2016)   0.3282     0.8574   0.383  0.1466  1   0.701853
scale(Foli.flo)    0.6738     0.7062   0.954  0.9104  1   0.340001
scale(PG.num)      0.7579     0.6990   1.084  1.1758  1   0.278212

                Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond19.null  7 177.65 187.46 -81.827   163.65
mod.cond19       8 169.73 180.94 -76.867   153.73 9.9203      1   0.001635 **

### Condition 23 ###
mod.cond23 <- glmmTMB((No.Sem) ~ scale(FD) + scale(Height) + scale(Foli.fru) +
scale(PG.num) + scale(Ov.num) + scale(Foli.flo) + scale(Flo) + (1 | Site), ziformula = ~1,
data = datos, family = gaussian)

                   Estimate Std. Error z value Pr(>|z|)
(Intercept)         1.72148    0.07664  22.463  < 2e-16 ***
scale(FD)          -0.70723    0.11669  -6.061 1.35e-09 ***
scale(Height)      -0.54081    0.07144  -7.570 3.73e-14 ***
scale(Foli.fru)    -0.66431    0.10945  -6.070 1.28e-09 ***
scale(PG.num)      -0.75987    0.08568  -8.868  < 2e-16 ***
scale(Ov.num)        0.15746    0.10162   1.550   0.1212
```

```
scale(Foli.flo)      -0.76375    0.10562  -7.231 4.79e-13 ***
scale(Flo)           -0.19427    0.08672  -2.240   0.0251 *

                Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond23.null 10 77.877 91.889 -28.938   57.877
mod.cond23      11 62.528 77.941 -20.264   40.528 17.349      1  3.111e-05 ***
```

Models integrating the smaller characters analysis *basis set*

```
mod.cond1 <- lme((Foli.fru) ~ scale(Foli.2016) + scale(Height) + scale(Foli.flo), random=
~1|Site, data=datos, weights=varIdent(form = ~ 1 | Site), control=list(maxIter=500), method
= "ML")
mod.cond1.null <- lme((Foli.fru) ~ scale(Height) + scale(Foli.flo), random= ~1|Site,
data=datos, weights=varIdent(form = ~ 1 | Site), control=list(maxIter=500), method = "ML")

               Model df       AIC       BIC   logLik   Test  L.Ratio p-value
mod.cond1          1  8 -103.3231 -92.11352 59.66155
mod.cond1.null     2  7 -103.1205 -93.31213 58.56026 1 vs 2 2.202584  0.1378

mod.cond2 <- glmmTMB(No.Sem ~ scale(Foli.2016) + scale(Height) + scale(Foli.fru) +
scale(PG.num) + scale(Ov.num) + (1 | Site), ziformula = ~ 1, data = datos, family =
poisson)
mod.cond2.null <- glmmTMB(No.Sem ~ scale(Height)
+ scale(Foli.fru) + scale(PG.num) + scale(Ov.num) + (1 | Site), ziformula = ~ 1, data =
datos, family = poisson)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond2.null  7 86.506 96.314 -36.253   72.506
mod.cond2       8 87.763 98.972 -35.881   71.763 0.7432      1     0.3886

mod.cond3 <- glmmTMB((Fru) ~ scale(Foli.2016) + scale(Height) + scale(Foli.fru) +
scale(PG.num) + scale(Flo) + scale(FD) + (1 | Site), ziformula = ~1, data = datos, family =
poisson)
mod.cond3.null <- glmmTMB((Fru) ~ scale(Height) + scale(Foli.fru) + scale(PG.num) +
scale(Flo) + scale(FD) + (1 | Site), ziformula = ~ 1, data = datos, family = poisson)
               Df    AIC    BIC  logLik deviance Chisq Chi Df Pr(>Chisq)
mod.cond3.null  8 95.455 106.66 -39.727   79.455
mod.cond3       9 97.421 110.03 -39.710   79.421 0.034      1     0.8537

mod.cond4 <- glmmTMB((No.Sem) ~ scale(Foli.flo) + scale(Height) + scale(Foli.2016) +
scale(Foli.fru) + scale(PG.num) + scale(Ov.num) + (1 | Site), ziformula = ~1, data = datos,
family = poisson)
mod.cond4.null <- glmmTMB((No.Sem) ~ scale(Height) + scale(Foli.2016) + scale(Foli.fru) +
scale(PG.num) + scale(Ov.num) + (1 | Site), ziformula = ~1, data = datos, family = poisson)

               Df    AIC     BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond4.null  8 87.763  98.972 -35.881   71.763
mod.cond4       9 89.116 101.727 -35.558   71.116 0.6468      1     0.4213

mod.cond5 <- glmmTMB((Fru) ~ scale(Foli.flo) + scale(Height) + scale(Foli.2016) +
scale(Foli.fru) + scale(PG.num) + scale(Flo) + scale(FD) + (1 | Site), ziformula = ~1, data
= datos, family = poisson)
mod.cond5.null <- glmmTMB((Fru) ~ scale(Height) + scale(Foli.2016) + scale(Foli.fru) +
scale(PG.num) + scale(Flo) + scale(FD)  + (1 | Site), ziformula = ~1, data = datos, family
= poisson)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond5.null  9 97.421 110.03 -39.710   79.421
mod.cond5      10 98.151 112.16 -39.076   78.151 1.2695      1     0.2599

mod.cond6 <- lmer(Foli.fru ~ scale(PG.siz) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + (1|Site), data=datos)
mod.cond6.null <- lmer(Foli.fru ~ scale(Height) + scale(Foli.2016) + scale(Foli.flo) +
(1|Site), data=datos)

               Df     AIC     BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond6.null  6 -101.43 -93.026 56.717  -113.43
mod.cond6       7 -100.52 -90.715 57.262  -114.52 1.0895      1     0.2966
```

```
mod.cond7 <- lme((PG.num) ~ scale(PG.siz) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo), weights = varPower(form = ~fitted(.)),random = ~1|Site,data=datos, method
= "ML")
mod.cond7.null <- lme((PG.num) ~ scale(Height) + scale(Foli.2016) + scale(Foli.flo),
weights = varPower(form = ~fitted(.)), random = ~1|Site,data=datos, method = "ML")

              Model df      AIC      BIC    logLik   Test   L.Ratio p-value
mod.cond7         1  8 440.3157 451.5253 -212.1578
mod.cond7.null    2  7 439.1802 448.9886 -212.5901 1 vs 2 0.8645619  0.3525

mod.cond8 <- lmer(Ov.num ~ scale(PG.siz) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + scale(PG.num) + (1|Site), data=datos)
mod.cond8.null <-lmer(Ov.num ~ scale(Height) + scale(Foli.2016) + scale(Foli.flo) +
scale(PG.num) + (1|Site), data=datos)

              Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond8.null  7 177.65 187.46 -81.827   163.65
mod.cond8       8 177.50 188.71 -80.752   161.50 2.1491      1     0.1427

mod.cond9 <- glmmTMB((No.Sem) ~ scale(PG.siz) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + scale(Foli.fru) + scale(PG.num) + scale(Ov.num) +  (1 | Site), ziformula
= ~1, data = datos, family = gaussian)
mod.cond9.null <- glmmTMB((No.Sem) ~ scale(Height) + scale(Foli.2016) + scale(Foli.flo) +
scale(Foli.fru) + scale(PG.num) + scale(Ov.num) + (1 | Site), ziformula = ~1, data = datos,
family = gaussian)

              Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond9.null 10 69.790 83.802 -24.895   49.790
mod.cond9      11 71.693 87.106 -24.846   49.693 0.0973      1     0.7551

mod.cond10<- lmer((PG.siz) ~ scale(Flo) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + (1|Site), data=datos)
mod.cond10.null<- lmer((PG.siz) ~ scale(Height) + scale(Foli.2016) + scale(Foli.flo) +
(1|Site), data=datos)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond10.null  6 151.67 160.08 -69.837   139.67
mod.cond10       7 150.26 160.07 -68.131   136.26 3.4112      1    0.06476 .

mod.cond11 <- lme((FD) ~ scale(PG.siz) + scale(Height)+ scale(Foli.2016) + scale(Foli.flo)
+ scale(Flo), random= ~1|Site, data=datos, method = "ML", weights=varIdent(form = ~ 1 |
Site), control=list(maxIter=500))
mod.cond11.null <- lme((FD) ~ scale(Height)+ scale(Foli.2016) + scale(Foli.flo) +
scale(Flo), random= ~1|Site, data=datos, method = "ML", weights=varIdent(form = ~ 1 |
Site), control=list(maxIter=500))

               Model df      AIC      BIC    logLik   Test   L.Ratio p-value
mod.cond11         1 10 71.71438 85.72636 -25.85719
mod.cond11.null    2  9 69.99286 82.60363 -25.99643 1 vs 2 0.2784726  0.5977

mod.cond12 <- glmmTMB((Fru) ~ scale(PG.siz) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + scale(Foli.fru) + scale(PG.num) + scale(Flo)
+ scale(FD) + (1 | Site), ziformula = ~1, data = datos, family = poisson)
mod.cond12.null <- glmmTMB((Fru) ~ scale(Height) + scale(Foli.2016) + scale(Foli.flo) +
scale(Foli.fru) + scale(PG.num) + scale(Flo)  + scale(FD) + (1 | Site), ziformula = ~1,
data = datos, family = poisson)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond12.null 10 98.151 112.16 -39.076   78.151
mod.cond12      11 99.310 114.72 -38.655   77.310 0.8413      1      0.359

mod.cond13 <- lme((PG.num) ~ scale(Foli.fru) + scale(Height) + scale(Foli.flo) +
scale(Foli.2016), weights = varPower(form = ~fitted(.)), random = ~1|Site,data=datos,
method = "ML")
mod.cond13.null <- lme((PG.num) ~ scale(Height) + scale(Foli.flo) + scale(Foli.2016),
weights = varPower(form = ~fitted(.)), random = ~1|Site,data=datos, method = "ML")

               Model df      AIC      BIC    logLik   Test   L.Ratio p-value
mod.cond13         1  8 440.9657 452.1753 -212.4829
mod.cond13.null    2  7 439.1802 448.9886 -212.5901 1 vs 2 0.2145127  0.6433
```

```
mod.cond14 <- lmer(Foli.fru ~ scale(Ov.num) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + scale(PG.num) + (1|Site), data=datos)
mod.cond14.null <- lmer(Foli.fru ~ scale(Height) + scale(Foli.2016) + scale(Foli.flo) +
scale(PG.num) + (1|Site), data=datos)

               Df      AIC     BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond14.null  7  -99.852 -90.044 56.926  -113.85
mod.cond14       8 -102.046 -90.836 59.023  -118.05 4.1935      1    0.04058 *

mod.cond15 <- glmer.nb((Flo) ~ scale(Foli.fru) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + (1|Site), data=datos)
mod.cond15.null <-glmer.nb((Flo) ~ scale(Height) + scale(Foli.2016) + scale(Foli.flo) +
(1|Site), data=datos)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond15.null  6 312.78 321.19 -150.39   300.78
mod.cond15       7 314.66 324.47 -150.33   300.66 0.1227      1     0.7261

mod.cond16 <- lme((Foli.fru) ~ scale(FD) + scale(Height)+ scale(Foli.2016) +
scale(Foli.flo) + scale(Flo), random= ~1|Site, data=datos, method = "ML",
weights=varIdent(form = ~ 1 | Site), control=list(maxIter=500))
mod.cond16.null <- lme((Foli.fru) ~ scale(Height)+ scale(Foli.2016) + scale(Foli.flo) +
scale(Flo), random= ~1|Site, data=datos, method = "ML", weights=varIdent(form = ~ 1 |
Site), control=list(maxIter=500))

               Model df       AIC        BIC   logLik   Test  L.Ratio p-value
mod.cond16         1 10 -110.5579  -96.54589 65.27893
mod.cond16.null    2  9 -118.4400 -105.82918 68.21998 1 vs 2 5.882096  0.0153

mod.cond17 <- glmer.nb((Flo) ~ scale(PG.num) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + (1|Site), data=datos)
mod.cond17.null <- glmer.nb((Flo) ~ scale(Height) + scale(Foli.2016) + scale(Foli.flo) +
(1|Site), data=datos)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond17.null  6 312.78 321.19 -150.39   300.78
mod.cond17       7 314.63 324.44 -150.32   300.63 0.1504      1     0.6981

mod.cond18 <- lme((FD) ~ scale(PG.num) + scale(Height)+ scale(Foli.2016) + scale(Foli.flo)
+ scale(Flo), random= ~1|Site, data=datos, method = "ML", weights=varIdent(form = ~ 1 |
Site), control=list(maxIter=500))
mod.cond18.null <- lme((FD) ~ scale(Height)+ scale(Foli.2016) + scale(Foli.flo) +
scale(Flo), random= ~1|Site, data=datos, method = "ML", weights=varIdent(form = ~ 1 |
Site), control=list(maxIter=500))

               Model df      AIC      BIC    logLik   Test   L.Ratio p-value
mod.cond18         1 10 71.43381 85.44578 -25.71691
mod.cond18.null    2  9 69.99286 82.60363 -25.99643 1 vs 2 0.5590464  0.4546

mod.cond19 <- lmer((Ov.num) ~ scale(Flo) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + scale(PG.num) + (1|Site), data=datos)
mod.cond19.null <- lmer((Ov.num) ~ scale(Height) + scale(Foli.2016) + scale(Foli.flo) +
scale(PG.num) + (1|Site), data=datos)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond19.null  7 177.65 187.46 -81.827   163.65
mod.cond19       8 169.73 180.94 -76.867   153.73 9.9203      1   0.001635 **

mod.cond20 <- lme((FD) ~ scale(Ov.num) + scale(Height)+ scale(Foli.2016) + scale(Foli.flo)
+ scale(PG.num) + scale(Flo), random= ~1|Site, data=datos, method = "ML",
weights=varIdent(form = ~ 1 | Site), control=list(maxIter=500))
mod.cond20.null <- lme((FD) ~ scale(Height)+ scale(Foli.2016) + scale(Foli.flo) +
scale(Flo) + scale(Flo), random= ~1|Site, data=datos, method = "ML", weights=varIdent(form
= ~ 1 | Site), control=list(maxIter=500))

               Model df      AIC      BIC    logLik   Test  L.Ratio p-value
mod.cond20         1 11 68.92348 84.33665 -23.46174
mod.cond20.null    2  9 69.99286 82.60363 -25.99643 1 vs 2 5.069375  0.0793
```

```
mod.cond21 <- glmmTMB((Fru) ~ scale(Ov.num) + scale(Height) + scale(Foli.2016) +
scale(Foli.flo) + scale(PG.num) + scale(Foli.fru) + scale(Flo) + scale(FD) + (1 | Site),
ziformula = ~1, data = datos, family = poisson)
mod.cond21.null <- glmmTMB((Fru) ~ scale(Height) + scale(Foli.2016) + scale(Foli.flo) +
scale(PG.num) + scale(Foli.fru) + scale(Flo) + scale(FD) + (1 | Site), ziformula = ~1, data
= datos, family = poisson)

               Df     AIC    BIC  logLik deviance Chisq Chi Df Pr(>Chisq)
mod.cond21.null 10  98.151 112.16 -39.076   78.151
mod.cond21      11 100.163 115.58 -39.081   78.163     0      1          1

mod.cond22 <- glmer.nb((Flo) ~ scale(No.Sem) + scale(Height) + scale(Foli.fru) +
scale(PG.num) + scale(Ov.num) + scale(Foli.2016) + scale(Foli.flo) + (1|Site), data=datos)
mod.cond22.null <- glmer.nb((Flo) ~ scale(Height) + scale(Foli.fru) + scale(PG.num) +
scale(Ov.num) + scale(Foli.2016) + scale(Foli.flo) + (1|Site), data=datos)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond22.null  9 308.38 320.99 -145.19   290.38
mod.cond22      10 307.37 321.38 -143.69   287.37 3.0073      1    0.08289 .

mod.cond23 <- glmmTMB((No.Sem) ~ scale(FD) + scale(Height)+ scale(Foli.fru) + scale(PG.num)
+ scale(Ov.num) + scale(Foli.flo) + scale(Flo) + (1 | Site), ziformula = ~1, data = datos,
family = gaussian)
mod.cond23.null <- glmmTMB((No.Sem) ~ scale(Height)+ scale(Foli.fru) + scale(PG.num) +
scale(Ov.num) + scale(Foli.flo) + scale(Flo) + (1 | Site), ziformula = ~1, data = datos,
family = gaussian)

               Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond23.null 10 77.877 91.889 -28.938   57.877
mod.cond23      11 62.528 77.941 -20.264   40.528 17.349      1  3.111e-05 ***

mod.cond24 <- glmmTMB((No.Sem) ~  scale(Fru) + scale(Height) + scale(Foli.fru) +
scale(PG.num) + scale(Ov.num) + scale(Flo) + scale(FD) + (1 | Site), ziformula = ~1, data =
datos, family = gaussian)
mod.cond24.null <- glmmTMB((No.Sem) ~ scale(Height) + scale(Foli.fru) + scale(PG.num) +
scale(Ov.num) + scale(Flo) + scale(FD) + (1 | Site), ziformula = ~1, data = datos, family =
gaussian)

               Df    AIC     BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod.cond24.null 10 83.962  97.974 -31.981   63.962
mod.cond24      11 85.691 101.104 -31.846   63.691 0.2704      1      0.603
```

R packages used

Packages for fitting mix models:

lme4: Douglas Bates, Martin Maechler, Ben Bolker, Steve Walker (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48.

nlme: Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2019). *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-143, https://CRAN.R-project.org/package=nlme.

Car: Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

MuMIn: Barton, K. (2009) Mu-MIn: Multi-model inference. R Package Version 0.12.2/r18. http://R-Forge.R-project.org/projects/mumin/

visreg: Breheny P, Burchett W (2017). "Visualization of Regression Models Using visreg." *The R Journal*, **9**(2), 56–71.

glmmTMB: Mollie E. Brooks, Kasper Kristensen, Koen J. van Benthem, Arni Magnusson, Casper W. Berg, Anders Nielsen, Hans J. Skaug, Martin Maechler and Benjamin M. Bolker (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal, 9(2), 378-400.

mgcv: Wood SN (2011). "Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models." *Journal of the Royal Statistical Society (B)*, **73**(1), 3-36.
ggploty2: H. Wickham. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, 2016.

ggstance: Lionel Henry, Hadley Wickham and Winston Chang (2016). ggstance: Horizontal 'ggplot2' Components. R package version 0.3. https://CRAN.R-project.org/package=ggstance

bbmle: Ben Bolker and R Development Core Team (2017). bbmle: Tools for General Maximum Likelihood Estimation. R package version 1.0.20. https://CRAN.R-project.org/package=bbmle

DHARMa: Florian Hartig (2018). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.2.0. https://CRAN.R-project.org/package=DHARMa

Packages for fitting path analysis as well as R_c^2 estimates:

ggm: Giovanni M. Marchetti, Mathias Drton and Kayvan Sadeghi (2015). ggm: Functions for graphical Markov models. R package version 2.3. https://CRAN.R-project.org/package=ggm

sjstats: Lüdecke D (2019). *sjstats: Statistical Functions for Regression Models (Version 0.17.7)*. https://CRAN.R-project.org/package=sjstats.

piecewiseSEM: Lefcheck, Jonathan S. (2016) piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution. 7(5): 573-579. DOI: 10.1111/2041-210X.12512

ANEXO S2

Variable	Estimación
Folivoria$_{16cu}$	Porcentaje de daño por planta
Folivoria$_{flo}$	Porcentaje de daño por planta
Folivoria$_{fru}$	Porcentaje de daño por planta
Sincronía	Número de individuos con los que coincide cada planta durante su periodo de floración
Precipitación	Milímetros acumulados desde el primer día hasta el último día de floración
Crecimiento vegetativo	Centímetros promedio que se elongaron las ramas marcadas por planta entre el inicio de la floración y final de la fructificación
Altura	Talla en centímetros estimada por planta
Inflorescencias	Número de inflorescencias presentes en las ramas marcadas
Flores	Número de flores que llegaron a la antesis en las inflorescencias marcadas
Infrutescencias	Número de infrutescencias logradas en las ramas marcadas
Frutos	Número de frutos logrados en las inflorescencias marcadas
Diámetro floral	Milímetros promedio por corola por planta
Tamaño del grano de polen	Micras promedio por grano de polen por planta
Número de óvulos	Número de óvulos promedio por gineceo por planta
Número de granos de polen	Número promedio de granos de polen por flor
Semillas	Número de semillas promedio por fruto por planta