

Chapter 11

Galling Insect Community Associated with *Copaifera langsdorffii* (Fabaceae): The Role of Inter- and Intra-annual Host Plant Phenology

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Abstract Super-host plants of galling insects are important systems for hypotheses testing. Plant phenology directly affects the gall community through the synchronism between the target organs development and insect attack, or indirectly by promoting changes in plant resource quality and/or quantity. This study focus on the effects of inter- and intra-annual variations in plant phenology on the galling insect community associated with the host plant *Copaifera langsdorffii*. The species *C. langsdorffii* is a super-host of galling insect that have supra-annual fruiting and broadly intra-annual variation in phenology. Supra-annual fruiting affected the resource allocation among vegetative growth, reproduction and production of chemical defenses. The galling insect community changed between reproductive and non-reproductive years of *C. langsdorffii*. Moreover, leaf biomass and gall richness and abundance were also affected by intra-annual variation in plant phenology. Finally, the possible roles of plant phenology on gall community associated with *C. langsdorffi* are discussed.

Keywords Cerrado • Gall dynamics • Gall seasonality • Host phenology • Host specificity • Insect galls • Plant phenology • Plant-animal interactions • Richness • Seasonality • Super-host • Tropical savanna

11.1 Introduction

The discovery of patterns in nature stimulate the generation of factually based hypotheses and further experimental test of these hypotheses (Price et al. 1998). One of the concerns among ecologists has been the search for patterns and the

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mechanisms that shape them (e.g., Huston 1979; Fernandes and Price 1988; Novotny and Basset 2005; Kozak and Wiens 2010). In this sense, while population ecology theory has reached relative advance in recent decades, community ecology still deserves more attention. Probably, the inherent complexity of the natural system is the main obstacle to community ecology development (Morin 2011).

The fact that in tropical systems the most species alive are arthropods associated with plants (Price et al. 1995) could elect these organisms as model for studies on community ecology. However, some other characteristics of the tropical insect assemblage (the majority of these arthropods still is poorly identifiable, the species occur in low density, the composition of local assemblage is highly variably and the species present low specificity with their host plant) difficult the replicates attainment optimal and constrain hypotheses test at community level (Basset et al. 1996; Novotny and Basset 2005; Lewinsohn and Roslin 2008; Novotny et al. 2006).

Herbivorous insects are composed of several feeding guilds (e.g. sap-sucking, chewing, mining, seed predators and galling insects), with different specialization levels on their host plant and habitat (Koricheva et al. 1998; Novotny and Basset 2005). For example, comparatively to free-feeding insects, galling insects generally are considered more specialized herbivores (Carneiro et al. 2009; Fagundes and Fernandes 2011). Moreover, the structure (gall) resulted of the galling insect plant interaction are sessile, and easily sampled. The galls generally occur in high density on their host plant (e.g. Costa et al. 2010) and gall form and size is dependent on plant tissue quality (Fagundes et al. 2005). These characteristics make this guild very suitable for studies at different levels of ecological organization.

In this scenario, super host plants of galling insects (*sensu* Veldtman and McGeoch 2003) emerge as interesting systems for the community ecologist. Several studies developed in tropical areas relate the occurrence of super host plant of galling insects across different phytofisionomies (e.g. Amazonian Forest: Almada and Fernandes 2011, Atlantic Forest: Santos et al. 2012, Dry Tropical Forest: Luz et al. 2012, Neotropical Savanna: Araújo 2011, Rupestrian Fields: Espírito-Santo et al. 2007, restinga: Maia and Oliveira 2010). Thus, the existence of super host plants of galling insects allows the test of hypotheses at the community level; within (e.g. Fagundes et al. 2005; Espírito-Santo et al. 2007; Costa et al. 2010) and across different habitats (e.g. Cuevas-Reyes et al. 2006; Silva et al. 2009; Fagundes and Fernandes 2011). However, the mechanisms that have driven the existence of super host plants remain unknown. In this study the focus is on the effects of intra and inter-annual variations in phenology of *Copaifera langsdorffii* (Fabaceae), a super host of galling insects with supra-annual mass fruiting and complete deciduousness, on their galling insect community structure.

Phenology describes the timing of transitions between stages in organisms' life cycles. Plant phenology vary among and within years and can affect the insect herbivores directly by synchronism between specific phenological stages and population dynamics of insects (How et al. 1993; Fox et al. 1997; Vitou et al. 2008) or indirectly, by determining the quality of plant tissues for herbivores (Jarzomski et al. 2000; Russel and Louda 2004; Coyle et al. 2010). Moreover, the supra annual phenology also produces variation in resource for herbivores between years of high and low plant reproduction (Obeso 2002; Forister 2005; Fagundes et al. 2013).

Thereby, plant phenology can dictate resource availability and quality to herbivores both within a growing season and throughout the life of trees with broad effect on plant-herbivores interactions.

Plant tissues are more adequate for insect development at a specific time in plant's phenology, generating a window of suitability in which plants are most adequate for insect herbivores development (Yukawa 2000; Mopper 2005; Yukawa and Akimoto 2006). Thus, insects using these resources during unfavorable phenological stages may suffer reduction on their performance (Forister 2005). For instance, galling insect emerging after leaf maturation, and even those using late-produced foliage, may have insufficient resource to ideal development before leaf abscission (Egan and Ott 2007; Hood and Ott 2010). Thereby, synchronization of consumers with the resources upon which they depend is of fundamental importance to consumer fitness.

Given the specific feeding habit of galling insects, one expects a distribution pattern synchronized with their host plants phenology (Fernandes 1990; Coyle et al. 2010). However, the nature of this phenological window, being it predictable or variable, broad or narrow, has a large impact on the evolutionary history of plant-herbivore interactions (Yukawa 2000; Egan and Ott 2007). In fact, the selection would favor galling insects that attack early bud-breaking plants if plants present high bud-breaking synchronism (e.g. Yukawa and Akimoto 2006). Alternatively, asynchronous bud-breaking within a plant population results in temporal isolation between herbivore allowing the formation of demes and sympatric gall speciation (see Mopper 2005; Egan and Ott 2007).

Supra-annual mass fruiting is another plant phenological behaviour that affect herbivorous insects by changes in plant tissue quality. In reproductive years, plants show reduction or suspension of other physiological processes as a result of the internal reallocation of resources for production of fruits (Isagi et al. 1997; Obeso 2002). This differential allocation of resources produces changes in the characteristics of plants (e.g., architecture, growth, and chemical compounds), which may extend their effects to higher trophic levels (Bazzaz et al. 1987; Obeso 2002; Stamp 2003).

Trade-offs between reproduction and growth seem to be a common phenomenon in higher order plants. During the development of fruits, plants may reduce or even stop their growth because the fruits are strong nutrient drains (Abrahamson and Caswell 1982; Larcher 1995). Additionally, the differential allocation of resources for reproduction or growth may affect the phenolic content in leaf tissues, as those physiological activities interfere in the carbon/nutrient balance of plants (Bryant et al. 1983; Herms and Mattson 1992). Consequently, the synthesis of carbon-based defence compounds will be affected with broad effects on herbivore insects (Bryant et al. 1983; Herms and Mattson 1992; Stamp 2003).

Copaifera langsdorffii Desf. (Fabaceae: Caesalpinioideae) is a tropical tree species that reaches heights of up to ten meters in the Brazilian Cerrado (savanna). Fruiting is supra-annual, i.e. years of intense fruit production are followed by years of little or no fructification (Souza and Fagundes 2014). The plant shows complete deciduousness in the dry season of the year (July to September) and emission of new leaves immediately after the fall of leaves that were produced in the

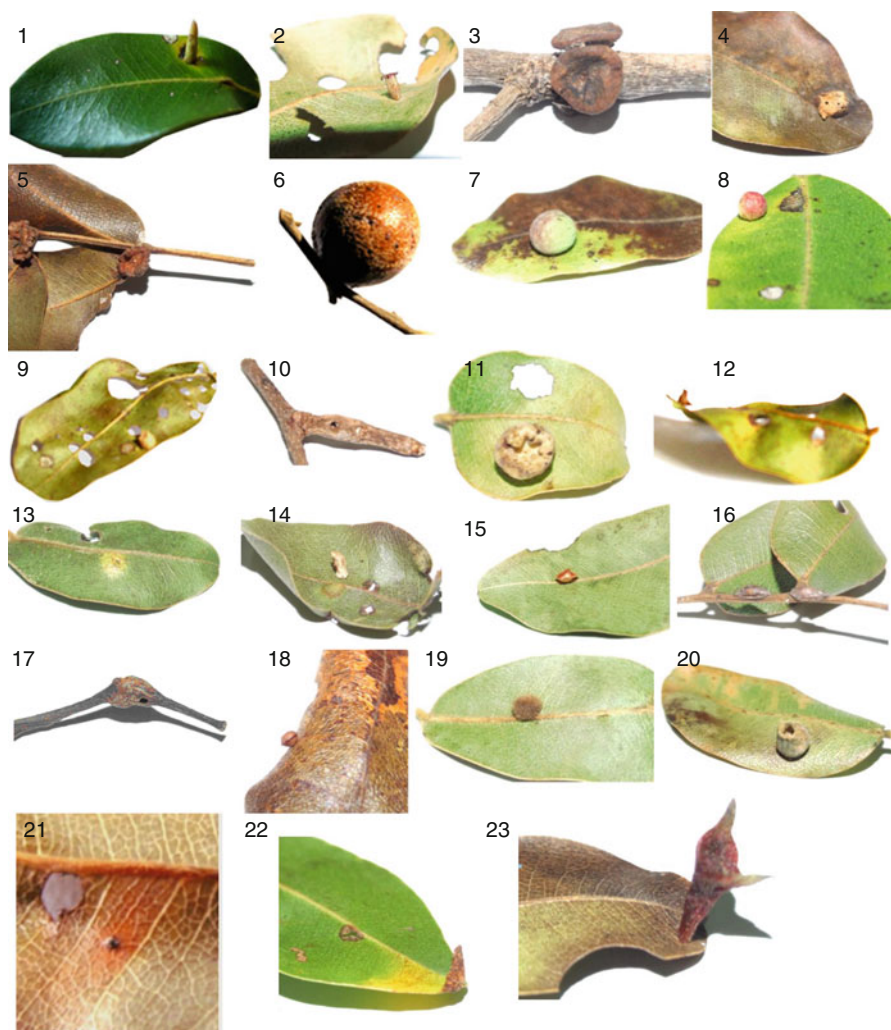


Fig. 11.1 Gall morphospecies collected from *Copaifera langsdorffii* in a cerrado (Brazilian Savanna) fragment, Minas Gerais, Brazil (After Costa et al. 2010)

previous year (Carvalho 2003). A total of 23 morphospecies of galls were found on *C. langsdorffii*, characterising the plant a super-host of galling insects (Costa et al. 2010, Fig. 11.1). Recent studies showed that plant ontogeny (see Costa et al. 2011) and plant tissue quality (Costa et al. 2011) may affect the gall community associated with *C. langsdorffii*. The leaves of *C. langsdorffii* grow slowly and leaflets have two extrafloral nectaries which are active only in the initial phase of leaf development (Costa et al. 2011). These extrafloral nectaries attract several ant species capable to inhibit herbivore attack on young leaves of *C. langsdorffii* (Queiroz et al. 2013).

This scenario lead us to expect that inter- and intra annual plant phenology (supra-annual fruiting and annual asynchronous leaf production after annual deciduousness, respectively) are important characteristics capable to shape the galling insect community associated with *C. langsdorffii*, both in ecological and evolutionary contexts. The study was conducted in a cerrado (Brazilian Savanna) fragment (16° 40'26'' S and 43° 48'44'' W) at the northern limit of the city of Montes Claros, Minas Gerais, Brazil. The region is inserted in the transition between the domains of Cerrado and Caatinga (Rizzini 1997). Usually, the Cerrado occurs in soils with low availability of nutrients that affect the characteristics of vegetation (Haridasan 1992) and its herbivore fauna (Neves et al. 2010). The local climate is of a semi-arid type, with well-defined dry and rainy seasons. The annual average temperature is of 23 °C, with rainfall of approximately 1.000 mm/year, concentrated rain mainly in the months of November to January (Santos et al. 2007). The soil of the study area is dystrophic with a developed herbaceous-subshrub layer, generally affected by fire (Costa et al. 2011; Fagundes et al. 2011).

11.1.1 Effects of Inter-annual Plant Phenology on Gallling Insects

During the month of March 2008, 35 *C. langsdorffii* individuals were selected and marked in the study area. Those individuals were from five to seven meters high, with a well-formed crown and in a good phytosanitary state (e.g. without presence of lianas or parasitic plants). All selected plants were monitored monthly during two consecutive years to determine the presence of flowers or fruits, thereby characterising the occurrence of a reproductive stage. All the marked individuals produced fruits in the first year, while none of them produced flowers or fruits in following year.

In May 2008 (period before deciduousness of leaves and when the vegetative growth of the species is completely) of each year of study, ten terminal branches were collected from all the selected plant individuals. The branches were collected at different points of the three crown to minimize possible microclimatic effects on plant growth or herbivores attack. Collected branches were approximately 30 cm long, corresponding to the plant growth of last season. Then, the branches were taken to the laboratory, where the following parameters were determined: the number of fruits, biomass of fruits, leaf biomass, and richness and abundance of galls. In addition, a total of 30 leaves per tree were collected to determine the tannin concentration in leaf tissues.

The number of fruits produced by the plants was determined by counting the fruits that were present in the ten sampled branches of each individual. To determine the biomass, the material was previously dried in an oven at 70°C for 72 h. After that, all branch fruits were weighed on an electronic precision scale. Similarly, all the leaves present in those ten branches were taken and weighed to determine leaf biomass. The method of radial diffusion was used to determine the tannin

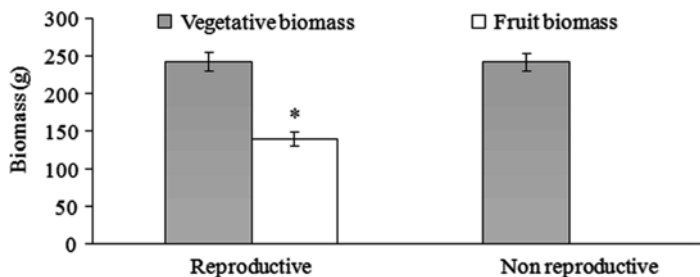


Fig. 11.2 Vegetative biomass (leaf and woody) and biomass of fruits produced by *C. langsdorffii* in the reproductive and non-reproductive year (n=35; average \pm SE; * represents significant differences between years)

concentration in *C. langsdorffii* leaves (Hagerman 1987). The richness and abundance of galls were determined by counting the number of galls present on the ten collected branches in each plant. The external morphology of galls was used to characterise and define each galling morphospecies (see Stone and Schönrogge 2003). Details of the characterisation and the determination of the galling insect morphospecies can be seen in Costa et al. (2010).

The population of *C. langsdorffii* studied presented intense fruit production in the first study year, followed by lack of fructification in the subsequent year (Fig. 11.2). In first year there was a production of 13.3 ± 5.8 (average \pm EP) fruits and 139.5 ± 53.8 g (average \pm EP) fruit biomass by collected branch. This fruit biomass corresponds to 57.6 % of the total vegetative biomass produced per individual of *C. langsdorffii* in 2008. Moreover, leaf biomass was 28.9 % higher in the non-reproductive year (Fig. 11.3a) while tannin concentration in the leaves of *C. langsdorffii* was approximately 157 % higher in the reproductive year (Fig. 11.3b).

There was a high inter-annual variation in the production of fruits by *C. langsdorffii*. This pattern of supra-annual fruiting seems to be common phenomenon in the *Copaifera* genus (Leite and Salomão 1992; Dias and Oliveira-Filho 1996; Pedroni et al. 2002). The study also showed that *C. langsdorffii* produced higher leaf biomass in non reproductive year and larger tannin production in reproductive years. Thus, based in the resource allocation theory (Herms and Mattson 1992) one would argue that higher investments in leaf biomass in non-reproductive year preclude tannin production because carbon is mainly allocated for vegetative growth.

In the reproductive year, 952 galls distributed into 18 galling morphospecies on *C. Langsdorffii* plants were found while in the non-reproductive year, 1,772 galls belonging to 19 morphospecies were collected. The total richness ($F=4.08$, $P=0.04$) and abundance ($F=11.49$, $P<0.01$) of galls associated with *C. langsdorffii* were 34.3 % and 85.7 % higher in the non-reproductive year, respectively (Fig. 11.4a, b). The increased galling species richness and abundance in the non-reproductive year can be associated to two factors: (1) in the non-reproductive year plants produced more leaves which resulted in more oviposition sites to galling females; and (2) in the reproductive year plants invested more resources in chemical defences, reducing the success of galling insect attack.

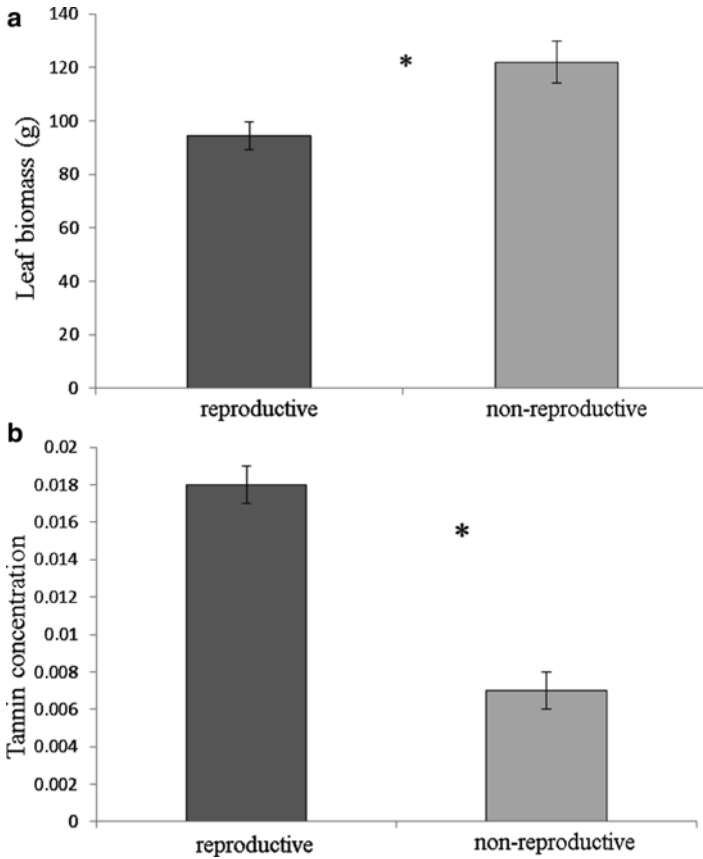


Fig. 11.3 Leaf biomass (a) and tannin concentration (b) produced by *Copaifera langsdorffii* in the reproductive year and in the non-reproductive year (n=35; average \pm SE; * represents significant differences between years)

Several studies were conducted with the objective of understanding the internal allocation of resources necessary to keep the costs of supra-annual reproductive cycles (e.g., Norton and Kelly 1988; Isagi et al. 1997; Satake and Iwasa 2000; Monks and Kelly 2006). However, no studies to date have attempted to characterise the ecological role of supra-annual fructification of tropical species and their effects in the allocation of resources inside the individual, what prevent us to extrapolate their effects in the different trophic levels. Some authors (e.g. Stamp 2003; Russel and Louda 2004; Kon et al. 2005; Tsvuura et al. 2011) suggest that supra-annual mass fruiting is an important plant strategy to reduce herbivore pressures. Although no experimental study was performed to date, it is reasonable to hypothesize that the supra-annual mass fruiting observed in *C. langsdorffii* affects gall community by changes in resource allocation.

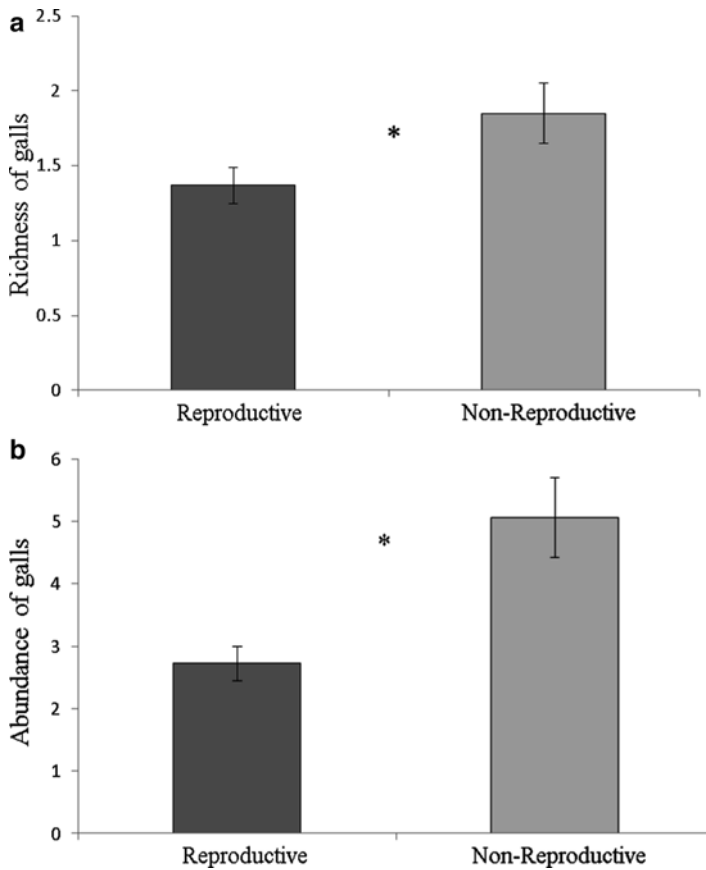


Fig. 11.4 Variation in gall insect richness (a) and abundance (b) collected from *Copaifera langsdorffii* branches between reproductive and non-reproductive years (n=35; average \pm SE; * represents significant differences between years)

11.1.2 Effects of Intra-annual Plant Phenology on Gall Insects

In order to characterize the effect of intra-annual variation in plant phenology on gall community associated with *C. langsdorffii* a total of 100 trees were selected and marked in the study area. All these plants were monitored weekly from July through October 2010 to access the period of leaf production. According the date of bud-breaking individual plants, trees were categorized into three phenological cohorts: *precocious plants* (tree that produced new

leaves before September, $n=24$); *intermediate plants* (trees that produced new leaves during September, $n=46$) and *delayed plants* (trees that produced new leaves after October, $n=31$).

During the May 2011, ten terminal branches were collected from all 100 marked plants ($n=1,000$). These branches were individually conditioned in plastic bags and taken to laboratory to determine leaf biomass, leaf tannin concentration, and gall richness and abundance per tree, as previously described. Insect galls collected from all branches were then categorized into morphospecies.

All plants monitored during this study did not show evidence of flower or fruit production, indicating that 2010 was a non-reproductive year for the *C. langsdorffii* population. Moreover, leaf biomass did not change among plant phenological cohorts ($F=0.048$, $P=0.640$). The presence of tannin was detected only in few plant individuals and hence the comparisons of leaf tannin concentration among plant cohorts were not considered in this study.

A total of 5,115 insect galls belonging to 21 morphospecies were collected from the 100 *C. langsdorffii* individuals. All gall morphospecies were observed on precocious and intermediated plants cohorts while morphospecies 1, 14, and 19 were not found on the delayed cohort plants (see Fig. 11.1 for galling morphospecies identification).

Gall richness ($Wald\ Stat=10.05$, $P<0.01$) and abundance ($Wald\ Stat=10.05$, $P<0.01$) varied among plant phenological cohorts. In fact, gall richness decreased on the delayed cohort plants (Fig. 11.5a) and total gall abundance was higher on the precocious cohort plants (Fig. 11.5b). However, at the population viewpoint we can detect variation species idiosyncratic attack on specific plant cohort. For instance, galling morphospecies 2, 4, 8, 9, 11 and 20 were more abundant on the precocious plant cohort while galling morphospecies 3 reached greater density on the delayed plant cohort (Fig. 11.6).

The results provide greater support for the contention that the galling insect community associated with *C. langsdorffii* is also affected by intra-annual variation in plant phenology. Many herbivores have adjusted their life cycle to synchronize their larval stadium with the appearance of target host tissues and organs (Fernandes 1990; Yukawa 2000). Female adults of galling insects primarily oviposit on undifferentiated tissues of host plant because their progeny must stimulate plant cell hyperplasia and hypertrophy, inducing the formation of the gall (Fernandes 1990; Cuevas-Reyes et al. 2006). Gallling insects emerging early or later budburst of the host plant experience reduction in their fitness because quality and quantity of available resource decay (Mopper 2005). Thus, adults of galling insects are restricted to a few days to find suitable sites to achieve their maximum fitness and larval characteristics are dictated by maternal host selection (Russel and Louda 2004; Cuevas-Reyes et al. 2006). This key issue on galling success/failure determine the population dynamics and the entire community organization (see Fernandes 1990); unfortunately it has been neglected in galling studies.

At the plants' perspective, the host species is able to reduce galling insect fitness escaping temporally the attack by the galling females. For example, adult

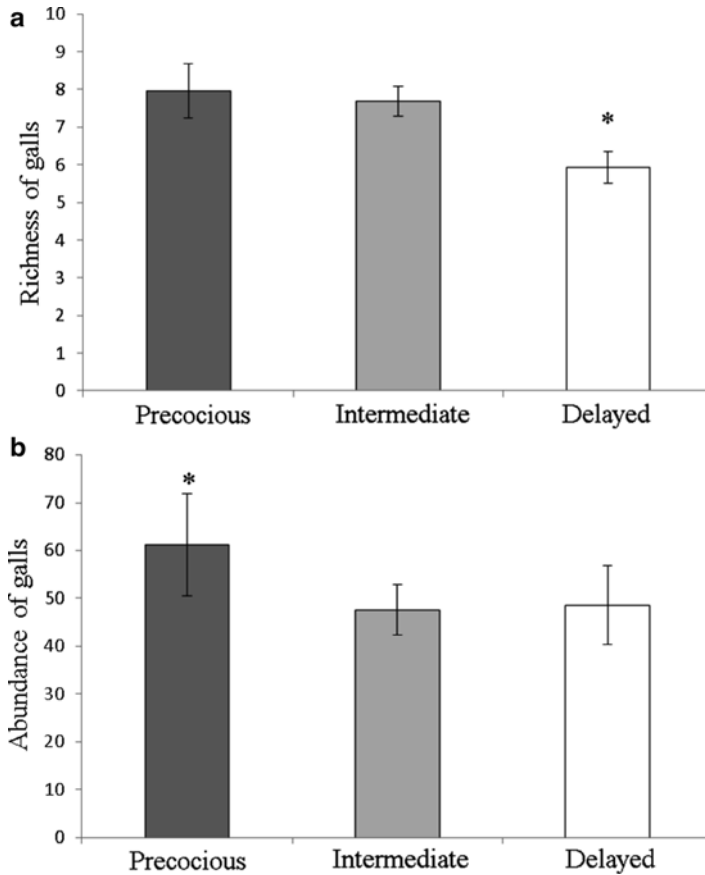


Fig. 11.5 Variation in gall richness (a) and abundance (b) collected from *Copaifera langsdorffii* branches among three plant phenological cohorts (average \pm SE; * represents significant differences)

emergency from the gall is not always synchronized with plant budbreaking if the plant population present unsynchronized leaf production. In fact, recent studies report that early budbreaking plants are more attacked by galling insects (Yukawa and Akimoto 2006). As a result, temporal variation in plant phenology can generate islands of adequate resources for galling insects allowing deme formation and sympatric speciation (Egan and Ott 2007). The studied population of *C. langsdorffii* showed broadly temporal variation in leaf flushing. The galling species associated with *C. langsdorffii* may show strong preference by specific phenological cohort. Thus, one can argue that intra-annual plant phenology is a possible element responsible by the high gall richness associated with *C. langsdorffii*.

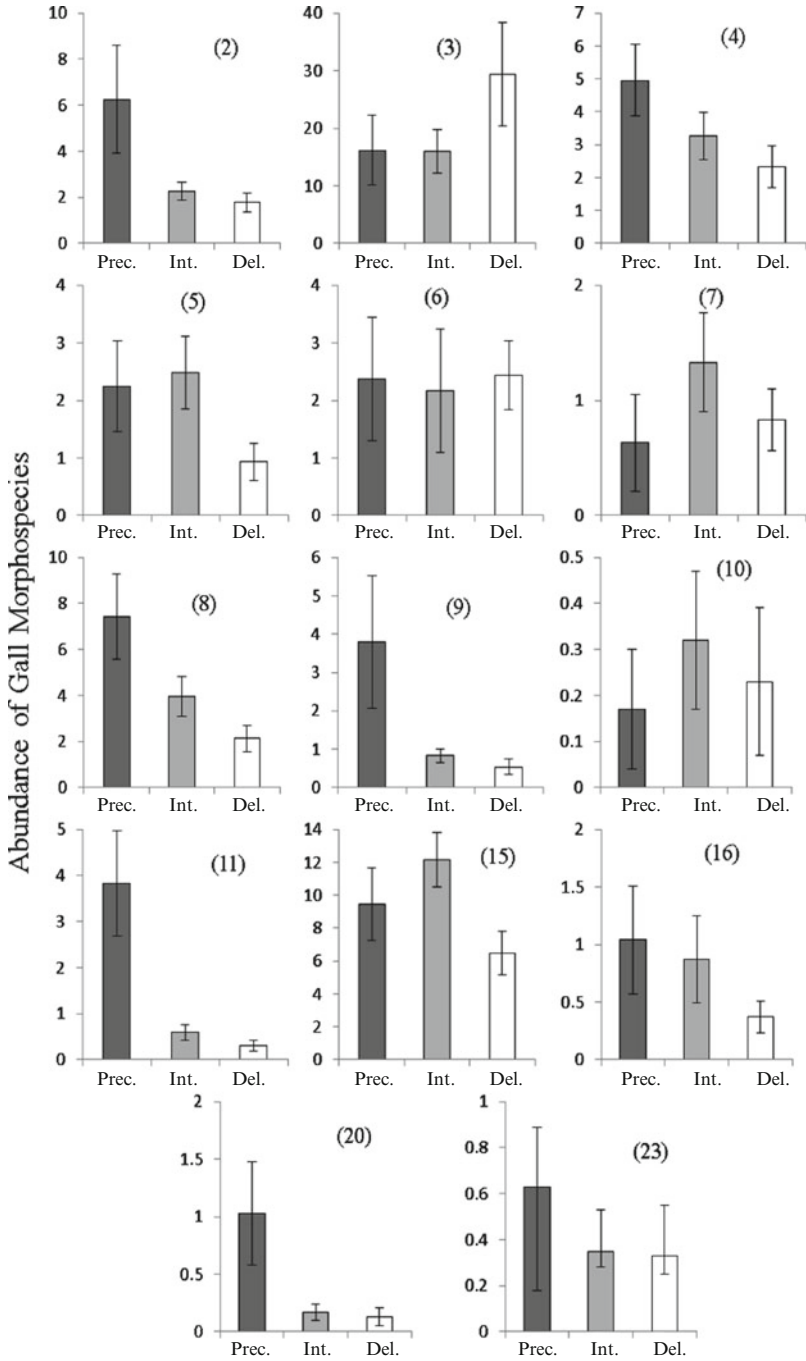


Fig. 11.6 Abundance (average \pm SE) of more frequent galls collected from *Copaifera langsdorffii* branches among three plant phenological cohorts (see Fig.11.1 for gall morphospecies identification)

11.2 Remarkable Conclusions

Copaifera langsdorffii is a super-host of galling insect that have supra-annual fruiting and broadly intra-annual variation in flushing leaves. Using this system, the present study calls attention for two relevant questions related to herbivore community organization. Firstly, the study suggests the possibility that inter- and intra-annual variation in plant phenology can be associated with herbivore community organization on *C. langsdorffii* both, in ecological and historical context. Second, the study also points out the possibly relationship between phenological asynchrony and the existent of super host plants. While some authors (see Egan and Ott 2007 and references therein) have stressed the importance of individual plant variation (e.g., phenology) on sympatric speciation of herbivores the debate about the factors that explain the existence of super host plants deserve more attention. In this study, these two questions are integrated and we suggest that variations inter- and intra-annual in plant phenology would determine high gall richness on *C. langsdorffii*.

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