Universidad de los Andes
Facultad de Ciencias
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Fig wasp diversity in three *Ficus* species and fig–wasp temporal association in *Ficusamericanaandicola*

Tesisparaoptar al título de Bióloga

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Nombrecompleto de el/los asesor/es: No aplica
Filiación del asesor: No aplica

Fecha:2deDiciembre de 2012

ABSTRACT

The system composed by *Ficus* and the wasps that pollinate them (Agaonidae) is considered as a mutualism whose strict one-to-one match seems to be repeatedly broken.The great specificity of the interaction is maintained by physical and chemical barriers such as ostiole diameter and volatiles that are thought to play an important role in the attraction of the wasps by the fig. It has been found that although the volatiles present in all *Ficus* species are the same, their proportion between species is different and remains constant among each species. However, there are few studies concerned with the actors of the multiple interactions and the time during which they interact in relation to the biology of the plant. The present paper assesses the fig–wasp temporal association in *Ficusamericanaandicola*and describes the diversity of wasps associated to three local *Ficus* species. A wasp sequence of arrival to the plant was determined and the pollinating and non-pollinating wasps were identified to genera.

Key words: *Ficusamericanaandicola, Ficustequendamae, Ficusgigantosyce, fig wasp,* temporal association, Agaonidae, mutualism

INTRODUCTION

Ficus and their pollinating wasps (Agaonidae) are considered as a mutualistic system and a coevolution model that originated roughly about 90 MYA(Machado et al., 2001; Datwyler and Weiblen, 2004). There are about 750 extant fig species of which at least 150 are native to South America and all of them are monoecious (Berg, 1989;Rønsted et al., 2008).

In monoecious species, the syconia bear both pistillate and staminate flowers and go through five different phases:first, the syconia develop and increase their size but the flowers and bracts are not well differentiated (pre-floral phase), then female flowers achieve maturity and the stigmas become receptive (female phase). At this time, one pollinating wasp enters eachsiconyum and lays eggs inside some of the ovaries while pollinating other flowersbefore it dies (Jousselin, 2003). In the inter-floral phase, seeds and wasps develop inside each syconium and emerge during the male phase when the staminate flowers are shading pollen. The male wasps fertilize the females and die but the females collect pollen and scape to other plants whose syconia are receptive where they complete their life cycle. Finally, the fruit ripens and the seeds are dispersed (post-floral phase) (Galil et al., 1968;Karunaratne, 2009; Weiblen, 2002).

Despite the general belief of aone-to-one matching of fig and pollinator species(Cook and Lopez-Vaamonde, 2001;Machado et al., 2005;Weiblen, 2001, Azuma et al., 2010), now it is believed thatthere may be more than one wasp species associated to one *Ficus* species (Cook andRasplus, 2003;Molbo et al., 2003), and evidence implyingthat at a fine

systematic scale, a strict co-speciation model would not adequately describe the system (Jackson et al.,2008).

Besides the many ways in which the interaction can be broken, there is the fact that this plant–insectinteractionbecomes more complex by the presence of non-pollinating fig wasps (NPFW) (Kerdelhué andRasplus, 1996). Those wasps may intervene in the system as parasites, parasitoids or hyperparasitoids and never enter the syconia but oviposit from the outside and develop inside some flower ovaries or induce galls in the fig receptacle thus, affecting the number of pollinating wasps and seeds produced by each syconium (Bronstein, 1988; Jandér and Herre, E.A., 2010; McLeish et al., 2010).

Interestingly, very few studies asses the time of arrival of the wasps considering the phenology of the plant, which is a very useful approach in order to determine the different biologies and reproductive strategies of the NPFW and the stability of the interaction (Elias et al., 2008).

The species included in these study were*Ficusamericanaandicola*whose syconia are up to 1.3 cm in diameter, *F. tequendamae* whose syconia are pubescent and up to 3 cm in diameter, both figs belong to the section Americana and thus are pollinated by wasps of the genus *Pegoscapus*, and *F. gigantosyce* whose great syconia reach up to 8 cm in diameter; this species belongs to the section Pharmacosycea and thus it is pollinated by wasps of the genus *Tetrapus* (Herre et al., 1996). All three systems could be considered could be all considered as a microcosmoswithinwhich multiple and intimate fig–wasp interactions take place.

Elucidating the very nature of those specific interactions has recently captivated the attention of biologists(Jansen-G. and Sarmiento, 2008; Cardona et al., 2007) as the systems appear as a potential source of knowledge because each*Ficus* species might be host for various undescribed wasps species.

The present study describes and compares the pollination systems in three local *Ficus* species by (1) determining the pollinating and NPFW diversity associated to the*Ficus* species and (2) establishing the fig–wasp temporal association to*F. americanaandicola.*

METHODS

- *Wasp diversity associated to three Ficus species*

The collecting time ranged from March to October 2011. Plant material from *Ficusamericanaandicola*and *F. tequendamae* was collected from trees located throughout Bogota city, Colombia (04°36′35″N, 74°04′54″W), and plant material from *F. gigantosyce* was collected from Hacienda Sabaneta, Municipio de Granada, Cundinamarca, Colombia (4°32´9.6´´N, 74°18´52.20´´W) at elevations between 2600 to 2720 m.a.s.l.

F. americanaandicola is distributed from the coastal mountain range of Venezuela through the Andes to northern Ecuador and was introduced in Bogotá (Berg, 2007), *F. tequendamae* is also associated to the Andes and was introduced in Bogotá too. However, *F. gigantosyce´*s trees sampled are native but reduced tosmall and isolated populations (A.M. Bedoya, personal observation).

The areas were inspected for trees whose syconia were ready for wasps to emerge (male phase). An average of 18, 17 and 14 syconia per tree for *F. americanaandicola*, *F. tequendamae*and *F. gigantosyce*were collected respectively and then each of them was

split open, placed in vials and covered with cloth secured by wrapping tightly a rubber band around each vial(G.D. Weiblen, personal communication). Wasp emerged within one week, were killed with acetone to get relaxed individuals and kept in 70% alcohol . Female wasps where then counted and identified to genus or familyby using Boucek´s identification key (1993), Gibson´s key to the genera of Nearctic Chalcidoidea (1997) and keys from the book of neotropical Hymenoptera by Fernando Fernandez (2006).

- *Fig–wasp temporal association in Ficusamericanaandicola*

The experiment was carried out at Universidad de los Andes´s campus, Bogotá, Colombia (04°36′35″N, 74°04′54″W). The campus includes one individual tree that was monitored from March to August, 2011.

In Bogotá, *F. americanaandicola* is pollinated by *Pegoscapusbacataensis* (Jansen-G & Sarmiento 2008) and 22 morphospecies of NPFW have been described as associated to the system (Cardona et al., 2007).

Five adhesive traps were installed in March according to the methods used by Elias *et al.*(2008) but with slight modifications. 350ml bottles were covered with entomological glue (Jerobiológicos©) and placed in the tree making sure it was uniformly covered. Adhesive traps were daily monitored from pre-floral to post-floral phase. The wasps trapped were removed by using a hypodermic needle and identified according to the same methods used to describe the diversity of wasps associated to the three *Ficus* species. At the same time, up to three syconia were randomly collected and split open to identify the phase of development by using the stereoscope and 34 syconia were measured every day in order to register the mean change in diameter.

RESULTS

- *Wasp diversity associated to three Ficus species*

There were six trees sampled and ±18 syconia collected per fig for a total of 107 syconia and 6138 wasps counted for *F. americanaandicola*. A total of five trees were sampled, ±17 syconia were collected per tree for a total of 86 syconia and 18771 wasps were counted for *F. tequendamae*,.A total of two trees of*F. gigantosyce* were sampled,14 syconia were collected and a total of 2393 wasps were counted; this low number of trees was due to the reduced number of individuals with wasps ready to emerge,

In *F. americanaandicola* the proportion of pollinating wasps was much higher than theNPFW except for very few cases in which there were no pollinating wasps inside the syconium but it was not aborted due to the presence of the non-pollinating *Aepocerus* which avoids syconium abortion(Fig. 1) (Bronstein, 1991; Compton, 1993). The species presence and number of NPFW individuals was highly variable within trees in the three *Ficus* species. In some of them, the presence of NPFW and the number of species was high while in others, there were no NPFW present (Fig. 1, Fig. 2)

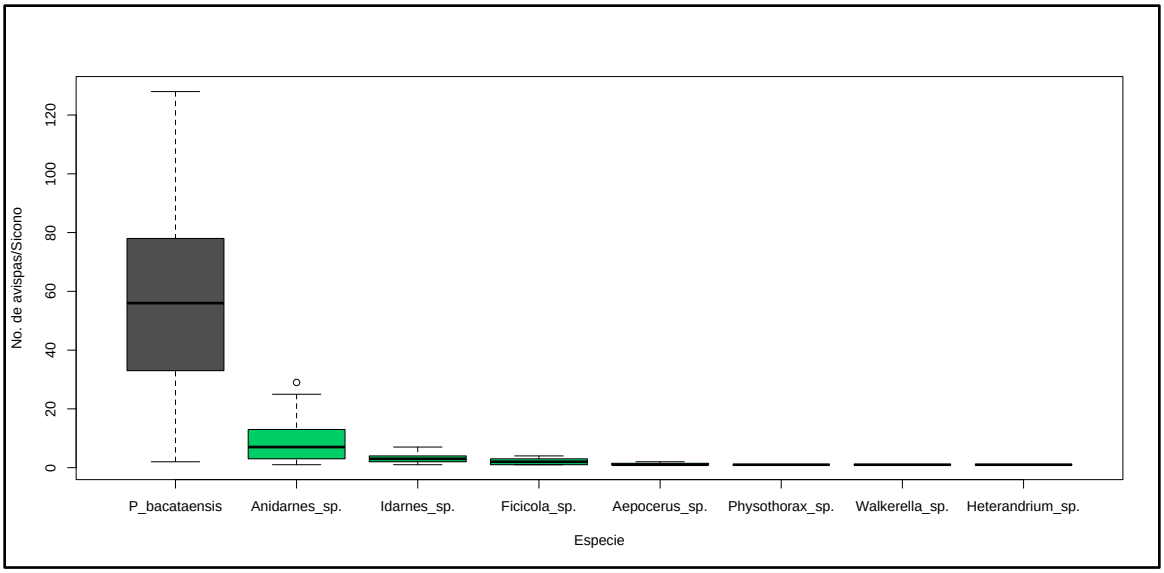

Figure 1. Proportion of pollinating (gray) and non-pollinating (green) fig wasps inside each syconium in *F. americanaandicola*. Central traces represent medians.

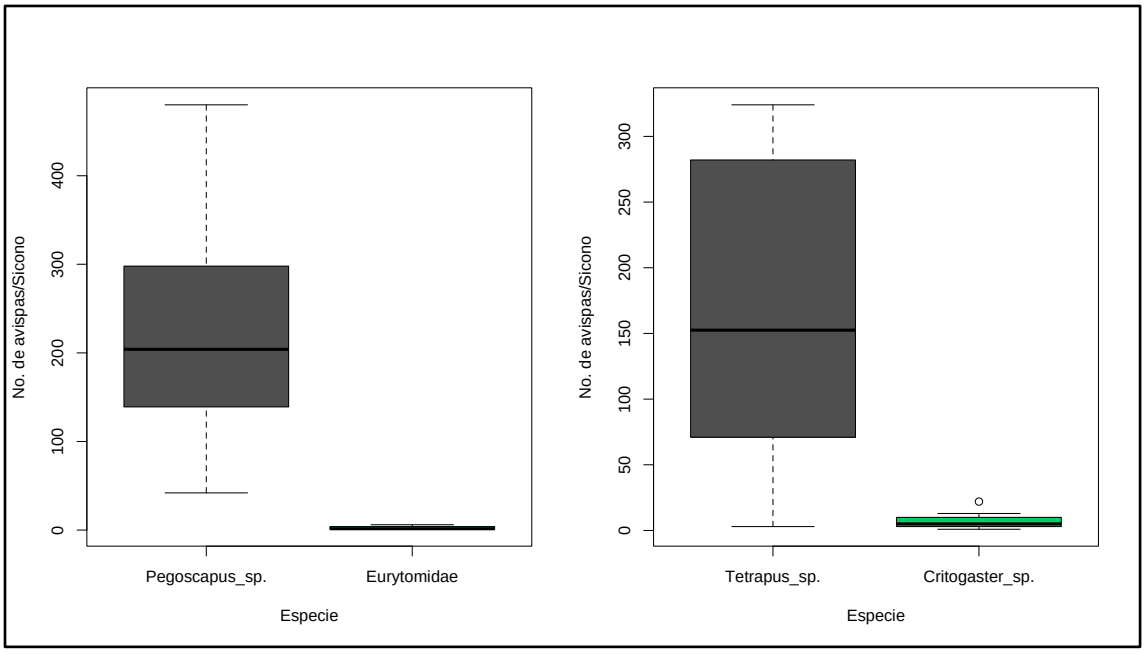

Figure 2. Proportion of pollinating (gray) and nonpollinating (green) fig wasps in *F. tequendamae*(left)and*F. gigantosyce*(right).

Pollinator species differ within the three *Ficus* species. *Pegoscapusbacataensis*(Jansen-G and Sarmiento, 2008)(Fig.3A),*Pegosapus*sp.(Fig.3G), *and Tetrapus*sp. (Fig.3I) were

found as the pollinator of *F. americanaandicola, F. tequendamae*and *F. gigantosyce* respectively. *F. americanaandicola* was the fig species associated to more NPFW with sevenmorphospecies associated whereas only onemorphospecies was found inside both *F. tequendamae*and *F. gigantosyce* (Fig.4).

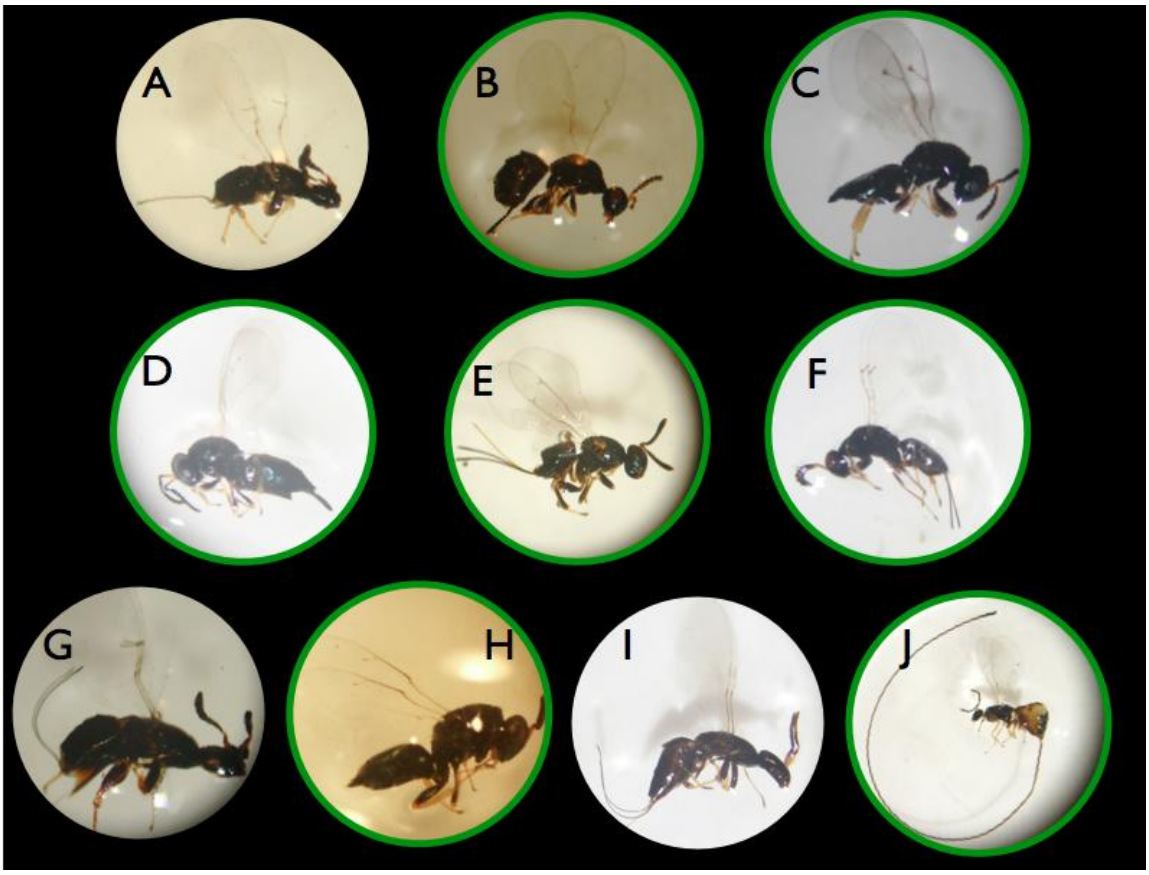

Figure 3. Pollinating (black-line circles) and non-pollinating (green-line circles) wasps associated to the three *Ficus* species. (A) *Pegoscapusbacataensis*, (B) *Anidarnes*sp., (C) *Ficicola*sp., (D) *Aepocerus*sp., (E) *Physothorax*sp., (F) *Idarnes*sp., (G)*Pegoscapus*sp., (H) Eurytomidae., (I) *Tetrapus*sp., (J) *Critogaster*sp.

Anidarnes(Fig.3B)was the more frequent NPFW present in *F. americanaandicola* followed by *Ficicola* (Fig. 3C), *Idarnes* (Fig. 3F), *Aepocerus* (Fig. 3D), Walkerella,

Heterandrium and *Physhothorax* (Fig. 3E) (Fig.4A). A species of wasps of the Eurytomidae family (Fig. 3H)was found associated to *F. tequendamae*(Fig.4B) and *Critogaster sp.*(Fig. 3J) was the only one found inside syconia of *F. gigantosyce* (Fig.4C).

The average number of pollinating wasps was 57, 218 and 174 per syconium in *F.americanaandicola*, *F.tequendamae* and *F. gigantosyce* respectively.

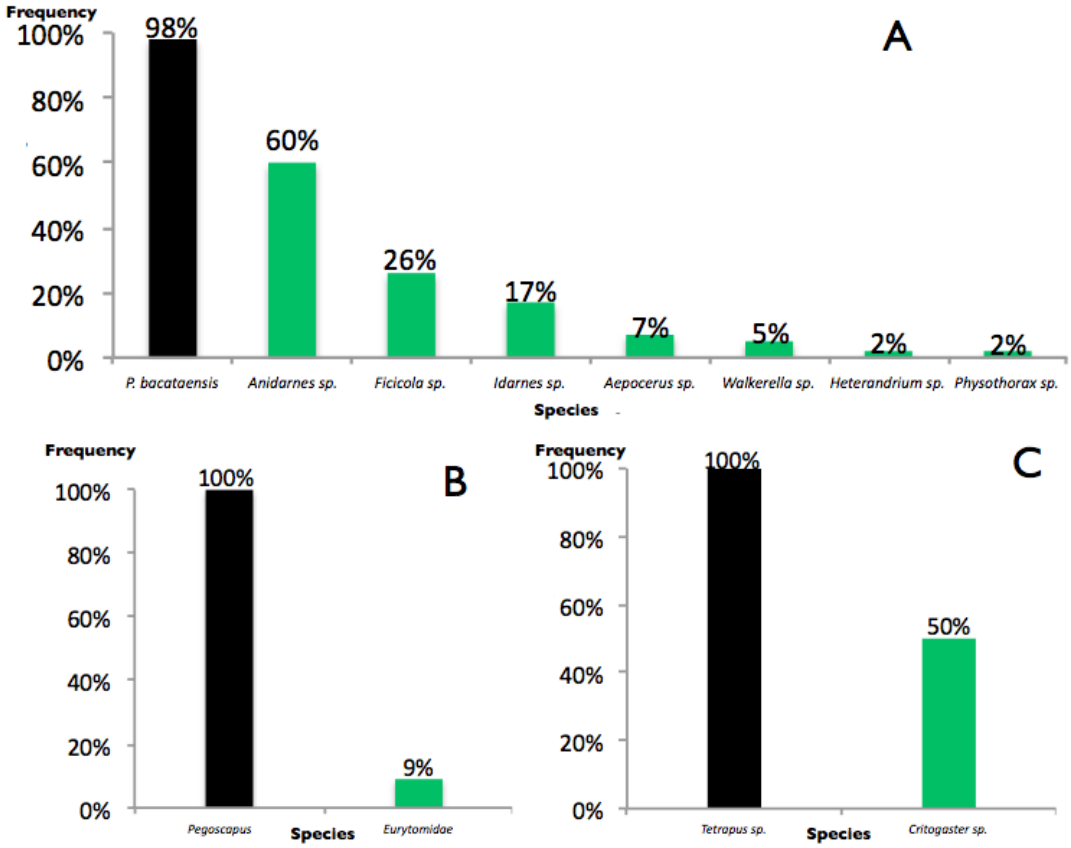

Figure. 4. Frequency of wasp species appearance in (A) *F. americanaandicola*, (B) *F. tequendamae* and (C) *F. gigantosyce.*

- *Fig–wasp temporal association in Ficusamericanaandicola*

There was an increase in the mean diameter of the syconia from 0.440 cm to 1.2 cm since

the beginning until the end of the experiment due to the maturation of the fruits. Phases A, B and C take 2, 2 and 4 months each. Lenticels appeared by the end of phase A and in the transition to phase B. These structures are thought to allow gas exchange between the inside and the outside of the syconium (Kuo–Huang and Hung, 1995). *Anidarnes* was the first wasp species recorded in the adhesive traps during both the late phase A and early phase B and was followed two days later by *Ficicola*.Ptermoalid wasps were trapped during phase B, but these could not be identified to genus due to the bad conditions of the specimens. Only two *Physotorax* individuals were captured along the middle of phase B and the last wasps captured belong to species*P.bacataensis*, whose time of appearance ranged from the middle of phase B, when most of the pistillate flowers are receptive, to the beginning of phase C. The number of wasps trapped each day was highly variable. Finally,syconia abortion events were recorded near the end of phase B and correspondto unpollinatedsyconia. The aborted fruits were located in the basal branches of the tree where no wasps were captured in the traps.

DISCUSSION

- *Wasp diversity associated to three Ficus species*

The occurrence frequency of NPFW in *F. americanaandicola*recorded in this study was different from the results showed by Cardona et al. in Otún, Quimbaya, Risaralda, Colombia in 2007. Cardona found that the most common NPFW was *Idarnes* (62%), followed by *Heterandrium* (43%), *Anidarnes* (12%),*Aepocerus* (8%), *Physothorax* (7%), and *Ficicola* (4%). The differences in the occurrence frequency can be due to the difference in study sites, which would imply that the NPFW associated to a *Ficus* species vary along the distribution range of the plant. However, the results in both the present

study and in the study of Cardona, show just a picture of what happened in a particular moment in time. Sarmiento (personal- comunication), collected syconia in different *F. americanaandicola* trees along 2007 and found that the occurrence frequency of the NPFW fluctuated in time. This could possibly account for variations in climatic factors such as sunshine, temperature, precipitation, wind, etc and could explain the difference between our results and Cardona´s.

The difference in NPFW diversity among the three *Ficus*species evaluated in this study reflects some kind of specificity of the non-pollinators to their hosts in spite of the lack of strictness in the interaction compared to that of the pollinator and its host. This specificity might be caused by: (1) volatile attraction, which means that the NPFW get attracted to the specific signal of the plant (this accounts for parasites and gallers), (2) the NPFW get attracted to the pollinator of the plant and use the volatiles emitted by the plant as a clue in order to get to the pollinator and parasitize it, or (3) physical barriers such as syconium size and receptacle width would restrict the ability of some species to oviposit from the outsider while favoring others. These three possibilities are not exclusive. However, the strength of the interaction between the plants and the NPFW is not as strong as it is between pollinators and their hosts and it is yet to be determined.

It is also important to mention that the small wasps pool found associated to *F. tequendamae* and *F. gigantosyce* could be a consequence of the small and isolated populations included in the study.

- *Fig–wasp temporal association in Ficusamericanaandicola*

The time of arrival of the wasps to the plant depends on: (1)phenological characters of 7the fig (lenticel presence, fruit size, stigma receptivity, etc) and (2) the resource

exploited by each wasp species (ovules, fig receptacle, wasps larvae, etc).

Lenticels were found to appear just before wasps first arrival, when syconia diameter increased significantly so we propose that besides gas exchange, lenticels may be involved in volatile emissions and thus, are implicated in the beginning of the fig–wasp association in time.

Fluctuations in the number of wasps trapped in time shows that even at a small scale, the number of wasps seems to be influenced by external factors such as sunsine, precipitation, temperature, and wind, among others.

The abortion of unpollinatedsyconia reflects a slight asynchrony in the maturation within a single tree, probably due to basipetal maturation,but also, depends on the location of the syconia in the fig.

ACKNOWLEDGMENTS

Thanks to Doctor Cornelis Berg and George Weiblenfor valuable help and comments. Special thanks to the Universidad de los Andes, Departamento de CienciasBiológicas and the staff of the Laboratorio de Botánica and the Laboratorio de sistemática y biologíacomparada de insectos at the Instituto de CienciasNaturales (ICN).

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Fig wasp diversity in three Ficus species and fig-wasp temporal association in Ficus americana andicola

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Número de páginas: 17

Ilustraciones: 4

MATERIAL ACOMPAÑANTE (Cantidad):

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*RESUMEN DEL TRABAJO DE GRADO:

The system composed by Ficus and the wasps that pollinate them (Agaonidae) is considered as a mutualism whose strict one-to-one match seems to be repeatedly broken. The great specificity of the interaction is maintained by physical and chemical barriers such as ostiole diameter and volatiles that are thought to play an important role in the attraction of the wasps by the fig. It has been found that although the volatiles present in all Ficus species are the same, their proportion between species is different and remains constant among each species. However, there are few studies concerned with the actors of the multiple interactions and the time during which they interact in relation to the biology of the plant. The present paper assesses the fig-wasp temporal association in Ficus americana andicola and describes the diversity of wasps associated to three local Ficus species. A wasp sequence of arrival to the plant was determined and the pollinating and non-pollinating wasps were identified to genera.

OBJETIVOS DEL TRABAJO DE GRADO:

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The areas were inspected for trees whose syconia were ready for wasps to emerge (male phase). An average of 18, 17 and 14 syconia per tree for F. americana andicola, F. tequendamae and F. gigantosyce were collected respectively and then each of them was split open, placed in vials and covered with cloth secured by wrapping tightly a rubber band around each vial (G.D. Weiblen, personal communication). Wasp emerged within one week, were killed with acetone to get relaxed individuals and kept in 70% alcohol . Female wasps where then counted and identified to genus or family by using Boucek´s identification key (1993), Gibson´s key to the genera of Nearctic Chalcidoidea (1997) and keys from the book of neotropical Hymenoptera by Fernando Fernandez (2006).

- Fig-wasp temporal association in Ficus americana andicola

The experiment was carried out at Universidad de los Andes´s campus, Bogotá, Colombia (04°36'35"N, 74°04'54"W). The campus includes one individual tree that was monitored from March to August, 2011.
In Bogotá, F. americana andicola is pollinated by Pegoscapus bacataensis (Jansen-G & Sarmiento 2008) and 22 morphospecies of NPFW have been described as associated to the system (Cardona et al., 2007).
Five adhesive traps were installed in March according to the methods used by Elias et al. (2008) but with slight modifications. 350ml bottles were covered with entomological glue (Jerobiológicos©) and placed in the tree making sure it was uniformly covered.
Adhesive traps were daily monitored from pre-floral to post-floral phase. The wasps trapped were removed by using a hypodermic needle and identified according to the same methods used to describe the diversity of wasps associated to the three Ficus species. At the same time, up to three syconia were randomly collected and split open to identify the phase of development by using the stereoscope and 34 syconia were measured every day in order to register the mean change in diameter.

CONCLUSIONES DEL TRABAJO DE GRADO:

- Wasp diversity associated to three Ficus species

The occurrence frequency of NPFW in F. americana andicola recorded in this study was different from the results showed by Cardona et al. in Otún, Quimbaya, Risaralda, Colombia in 2007. Cardona found that the most common NPFW was Idarnes (62%), followed by Heterandrium (43%), Anidarnes (12%), Aepocerus (8%), Physothorax (7%), and Ficicola (4%). The differences in the occurrence frequency can be due to the difference in study sites, which would imply that the NPFW associated to a Ficus species vary along the distribution range of the plant. However, the results in both the present study and in the study of Cardona, show just a picture of what happened in a particular moment in time. Sarmiento (personal-comunication), collected syconia in different F. americana andicola trees along 2007 and found that the occurrence frequency of the NPFW fluctuated in time. This could possibly account for variations in climatic factors such as sunshine, temperature, precipitation, wind, etc and could explain the difference between our results and Cardona´s.
The difference in NPFW diversity among the three Ficus species evaluated in this study reflects some kind of specificity of the non-pollinators to their hosts in spite of the lack of strictness in the interaction compared to that of the pollinator and its host. This specificity might be caused by: (1) volatile attraction, which means that the NPFW get attracted to the specific signal of the plant (this accounts for parasites and gallers), (2) the NPFW get attracted to the pollinator of the plant and use the volatiles emitted by the plant as a clue in order to get to the pollinator and parasitize it, or (3) physical barriers such as syconium size and receptacle width would restrict the ability of some species to oviposit from the outsider while favoring others. These three possibilities are not exclusive. However, the strength of the interaction between the plants and the NPFW is not as strong as it is between pollinators and their hosts and it is yet to be determined.
It is also important to mention that the small wasps pool found associated to F. tequendamae and F. gigantosyce could be a consequence of the small and isolated populations included in the study.

- Fig-wasp temporal association in Ficus americana andicola

The time of arrival of the wasps to the plant depends on: (1)phenological characters of the fig (lenticel presence, fruit size, stigma receptivity, etc) and (2) the resource exploited by each wasp species (ovules, fig receptacle, wasps larvae, etc).
Lenticels were found to appear just before wasps first arrival, when syconia diameter increased significantly so we propose that besides gas exchange, lenticels may be involved in volatile emissions and thus, are implicated in the beginning of the fig-wasp association in time.
Fluctuations in the number of wasps trapped in time shows that even at a small scale, the number of wasps seems to be influenced by external factors such as sunsine, precipitation, temperature, and wind, among others.
The abortion of unpollinated syconia reflects a slight asynchrony in the maturation within a single tree, probably due to basipetal maturation, but also, depends on the location of the syconia in the fig.

*PALABRAS CLAVES (TEMAS) DEL TRABAJO DE GRADO:

Ficus americana andicola, Ficus tequendamae, Ficus gigantosyce, fig wasp, temporal association, Agaonidae, mutualism

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