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Factors affecting nectar sugar composition in chiropterophilic plants

Factores que afectan la composición de azúcares en el néctar de plantas quiropterofílicas

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Abstract

Most pollinators prefer the sugars present in the nectar they consume, so it has been hypothesized that they have molded nectar trait evolution. However, nectar-feeding bats do not exhibit preferences for the sugars present in their diet. We analyzed the role that biochemical and ecological factors could play in shaping the nectar traits of chiropterophilic plants. We studied nectar traits and flower production in 49 plant species. We evaluated the relationship between nectar concentration and sugar composition using phylogenetically independent contrasts and if nectar traits were related to flower production using a Manova. We found that 42 species produced high hexoses nectars, and 7 species produced sucrose rich nectars. Phylogenetically independent contrasts showed that nectar concentration was negatively related to glucose content, positively related to fructose content, and was not related to sucrose content. A negative relationship was found from glucose and fructose contents to sucrose content, and glucose content was negatively related to fructose content. Finally, we did not found any relationship between nectar traits and the plants' flowering strategies. We conclude that bat physiology and the relative low evolutionary time of the interaction between plants and bats may determine the lack of pattern in the nectar characteristics of chiropterophilic plants.

Keywords: Chiropterophilic plants; Ecological factors; Nectar biochemistry; Nectar sugar composition

Resumen

La mayoría de los polinizadores prefieren los azúcares presentes en el néctar que consumen, por lo que se ha especulado que estos han moldeado la evolución de los rasgos del néctar. Sin embargo, los murciélagos nectarívoros no muestran preferencias por los azúcares presentes en su dieta. Analizamos el papel que los factores bioquímicos y ecológicos pueden desempeñar en los rasgos de néctar de 32 plantas quirotperofílicas. Se estudiaron las características del néctar y la producción de flores en 49 especies de plantas. Se evaluó la relación entre la concentración del néctar y la composición de azúcares usando contrastes filogenéticamente independientes y si los rasgos del néctar están relacionados con la producción de flores utilizando una Manova. Se encontró que 42 especies producen néctares con altos contenidos de hexosas y 7 especies producen néctares ricos

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en sacarosa. Los contrastes filogenéticamente independientes mostraron que la concentración de néctar se relaciona negativamente con el contenido de glucosa, positivamente con el de fructosa y no tuvo relación con el contenido de sacarosa. Se encontró una relación negativa del contenido de glucosa y fructosa con el de sacarosa y el contenido de glucosa se relacionó negativamente con el de fructosa. Por último, no encontramos ninguna relación entre los rasgos de néctar y las estrategias de floración. Concluimos que la fisiología de los murciélagos y el poco tiempo evolutivo de la interacción entre las plantas y los murciélagos pueden determinar la falta de patrón en los rasgos del néctar quiropterofílico.

Palabras clave: Plantas quiropterofílicas; Factores ecológicos; Bioquímica del néctar; Composición de azúcar del néctar

Introduction

Nectar constitutes the most important energy source that plants offer to pollinators (Simpson & Neff, 1983). The 3 most common and abundant sugars in nectar are by far the hexose monosaccharides glucose and fructose, and the disaccharide sucrose (Baker & Baker, 1983). The sugar composition and other characteristics of nectar vary with biochemical, ecological and evolutionary factors (Baker, Baker, & Hodges, 1998; Nicolson, 1998; Ornelas, Ordano, De-Nova, Quintero, & Garland, 2007).

Biochemically, sugar composition of nectar may vary due to changes in the activity of nectary enzymes and to osmoregulation processes caused by the osmotic pressure generated by the different sugars (Nicolson, 1998; Nicolson & Flemin, 2003). Nectar sugars are derived from sucrose translocated in phloem sap. Sucrose is either secreted into nectar, or it is hydrolyzed in the nectary walls by the activity of invertase enzymes into glucose and fructose (De la Barrera & Nobel, 2004; Nicolson, 2002). As a result, the final sugar composition of nectar is determined by both the activity and amount of invertase enzyme in the nectary (Sturm & Guo-Qing, 1999; Woodson & Wang, 1987). Sucrose hydrolysis into hexoses may increase nectar osmolality, causing water to move from the nectary walls into nectar and thus resulting in more dilute nectars (Nicolson, 1998, 2002). As consequence, nectar sugar composition could affect other nectar traits such as volume and concentration. For example, a dichotomy among volume and concentration with sugar composition has been observed in bird-pollinated flowers in which dilute and copious nectar is generally hexose-rich, while concentrated and less copious nectar is usually sucrose-rich (Baker & Baker, 1983; Lotz & Schondube, 2006; Martínez-del Río, Baker, & Baker, 1992; Nicolson, 1998; Nicolson & Flemin, 2003). Nevertheless, this pattern has not been evaluated for chiropterophilic plants.

The variation in sugar composition, nectar volume and nectar sugar concentration also are affected at ecological and evolutionary levels by plant mechanisms that are selected based on nectar production costs and by their pollinators' physiology. Several authors have stated that nectar production is costly for plants in terms of the amount of energy invested (Ashman & Shoen, 1997; Pleasants & Chaplin, 1983; Southwick, 1984). However, it has also been suggested that nectar production could have small energetic costs (Golubov, Mandujano, Montaña, López-Portillo, & Eguiarte, 2004; Pyke, 1992). Differences in nectar volume on the basis of a cost–benefit balance, has been also explained in which plants are "fitter" when they produce the smallest possible nectar volume to attract their pollinators (Lanza, Smith, Sack, & Cash, 1995).

Additionally, preferences of nectar-feeding foragers, based both on their morphology and physiology, also could have selective effects on the evolution of nectar characteristics (Baker & Baker, 1983; Baker et al., 1998; Erhardt, 1991; Faegri & van der Pijl, 1979; Heinrich & Raven, 1972; Martínez-del Río, Stevens, Daneke, & Andreadis, 1988; Martínez-del Río et al., 1992; Martínez-del Río, Schondube, & McWhorter, 2001; Ornelas et al., 2007). However, in the case of Neotropical nectarivorous bats, no evidence has been found of bats preferring the dominant sugars (glucose and fructose) present in the nectar they commonly ingest in nature (Herrera, 1999; Rodríguez-Peña et al., 2007). These findings cast a shadow of doubt on the validity of the hypothesis that bats' preferences could act as a selective pressure on the nectar composition of the plants they visit. The prevalence of hexose-dominated nectars among bat-pollinated plants in the Neotropics is an ecological pattern that remains to be explained.

The goal of our study was to analyze nectar traits (i.e. nectar sugar composition and concentration) of chiropterophilic plants, and use this information to understand how these traits could be influenced by biochemical and ecological factors. We analyzed data on the nectar traits of 49 Neotropical plant species that present chiropterophilic flowers. We used the data to evaluate: (1) the relationship between nectar traits (nectar concentration and sugar composition), and (2) the relationship between nectar traits and flowering strategies. First, we hypothesized that because chiropterophilic plant species produce dilute nectars with a greater proportion of hexoses than sucrose (Baker et al., 1998), the nectar concentration will be positively related with sucrose and negatively related with glucose and fructose (Nicolson, 1998). Second, because the hydrolysis of sucrose produces 1 molecule of glucose and 1 molecule of fructose (Nicolson, 2002), chiropterophilic nectars will show equal amounts of glucose and fructose, and the content of hexoses will show a negative relationship with the content of sucrose. Third, because flowering strategies and nectar traits are related to reproductive costs (Southwick, 1984), we predicted that plant species with high flower production should produce dilute nectar with low sucrose proportions, whereas plant species with low flower production will produce more concentrated nectar with greater sucrose proportions.