Rodriguésia 74: e01012022. 2023
http://rodriguesia.jbrj.gov.br
DOI: http://dx.doi.org/10.1590/2175-7860202374030

Review Paper

Reproductive biology of *Piper* species (Piperaceae): a review to link the past to the future

Adriano Valentin-Silva[1,2]

Abstract

Piper species are important components of the understory in tropical and subtropical forests, and some species are of economic and medicinal importance. This genus has been studied in different areas of science. However, some questions remain unanswered after the new circumscription as proposed by phylogenetic studies. Here, I review different aspects related to the reproductive biology of *Piper* species (phenology, sexual expression, floral biology, pollination and mating systems), comparing the results between Neotropical (representing most of the studies carried out so far) and Paleotropical regions. Seventy-five species were analyzed. Some patterns can be observed, mainly in Neotropical species, such as the predominance of annual flowering and fruiting, dichogamy (generally incomplete protogyny) with gradual and sequential exposure of stigmas, asynchronous pollen release, and pollination by insects. Some aspects have been poorly studied, such as variations in sexual expression, the efficiency of different pollinators, and the chemical composition of floral volatiles associated with their role in pollination. In addition, I discuss remaining gaps and further studies that are required, mainly on Paleotropical *Piper* species, to obtain basic information on the reproductive biology of these plants. From this, comparisons with Neotropical species can be made, allowing the verification of patterns in this genus.
Key words: floral biology, mating system, phenology, pollination, sexual expression.

Resumo

Espécies de *Piper* são importantes componentes do sub-bosque em florestas tropicais e subtropicais, e algumas espécies são de importância econômica e medicinal. Esse gênero tem sido estudado em diferentes áreas da ciência. No entanto, algumas questões permanecem sem resposta após a nova circunscrição proposta pelos estudos filogenéticos. Aqui, reviso diferentes aspectos relacionados à biologia reprodutiva das espécies de *Piper* (fenologia, expressão sexual, biologia floral, sistemas de polinização e reprodutivo), comparando os resultados entre as regiões neotropical (representando a maioria dos estudos realizados até agora) e paleotropical. 75 espécies foram analisadas. Alguns padrões podem ser observados, principalmente em espécies neotropicais, como a predominância de floração e frutificação anual, dicogamia (geralmente protoginia incompleta) com exposição gradual e sequencial dos estigmas, liberação assíncrona de pólen e polinização por insetos. Alguns aspectos têm sido pouco estudados, como as variações na expressão sexual, a eficiência dos diferentes polinizadores e a composição química dos voláteis florais associados ao seu papel na polinização. Além disso, discuto as lacunas remanescentes e são necessários mais estudos, principalmente sobre as espécies de *Piper* paleotropicais, para obter informações básicas sobre a biologia reprodutiva dessas plantas. A partir disso, comparações com espécies neotropicais podem ser feitas, permitindo a verificação de padrões nesse gênero.
Palavras-chave: biologia floral, sistema reprodutivo, fenologia, polinização, expressão sexual.

Introduction

Piper has a predominantly Pantropical distribution, although it occurs in some subtropical regions (Jaramillo & Manos 2001). It has over 2,100 species and is the second-largest genus of angiosperms (Simmonds *et al.* 2021), with the highest diversity of species occurring in tropical America (700 species) and South Asia (300 species)

See supplementary material at <https://doi.org/10.6084/m9.figshare.22626970.v1>

---

[1] Universidade Federal de Minas Gerais, Depto. Botânica, Av. Antônio Carlos 6627, 31270-901, Belo Horizonte, MG, Brasil. ORCID: <https://orcid.org/0000-0002-9206-8939>.
[2] Author for correspondence: adrianovalentin86@gmail.com

(Jaramillo & Manos 2001). Species of this genus grow as shrubs, herbs, climbers, or treelets, and are important components of the understory in tropical forests (Hartshorn & Hammel 1994; Greig 2004). Some species are of economic importance, such as *Piper nigrum* L. (black pepper), which is used worldwide as a condiment (Greig 2004), and *P. betle* L. (betel vine) and *P. methysticum* G. Forst. (kava kava) which are used medicinally (Di Stasi *et al.* 2002; Dyer *et al.* 2004). Studies on the genus *Piper* have been conducted in several areas of science. In 2004, the book "*Piper*: a model genus for studies of phytochemistry, ecology, and evolution" was published, which addresses different ecological and evolutionary aspects, such as mutualistic interactions with ants (Letourneau 2004) and bats (Fleming 2004), in addition to aspects of pollination biology (Figueiredo & Sazima 2004). Despite the existing knowledge of this genus, some questions remain to be answered, especially after phylogenetic studies have redefined the circumscription of the genus (Jaramillo & Manos 2001; Jaramillo *et al.* 2008).

The systematics of Piperaceae has changed over time since Kunth's work in 1839, changing the number of genera within this family, in addition to the use of infrageneric groups or sections in some taxonomic treatises (see a summary of the taxonomic history of *Piper* by Jaramillo & Manos 2001; Sen & Rengaian 2022). After phylogenetic studies using sequences from the ITS region and chloroplast intron *psbJ-petA* (Jaramillo & Manos 2001; Jaramillo *et al.* 2008), the circumscription of *Piper* was altered to incorporate further genera. Three major clades are recognized, corresponding to the geographic distribution of the species. Neotropical species are divided into eight subclades, most of which are currently considered subgenera: *Macrostachys*, *Radula*, *Peltobryon*, *Pothomorphe*, *Enckea*, *Ottonia*, *Schilleria*, and the *P. cinereum*/*P. sanctum* complex, all of which are hermaphroditic (bisexual flowers) and are considered a basal group (Jaramillo *et al.* 2008; Sen & Rengaian 2022). By contrast, Paleotropical species are categorized into two geographic clades, *i.e.*, tropical Asia (*Piper s.s.*) and the South Pacific (*Macropiper*), which produce unisexual flowers and are predominantly dioecious. Recent studies have evaluated the phylogeny of Asian pipers and found 17 infrageneric groups that constitute a sister group to the South Pacific group (Asmarayani 2018; Sen *et al.* 2019).

Here, I review the different aspects of reproductive biology of *Piper*, especially those related to pollination. I compare Neotropical with Paleotropical species and discuss knowledge gaps and potential topics for future studies.

Reproductive phenology

Phenological studies of *Piper* species have been conducted mainly in the Neotropical region. Here, I address reproductive phenophases of 67 species (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.22626970.v1>). However, there are studies that have examined leaf production in Neotropical (Marquis 1988; Angulo-Sandoval & Aide 2000; Thies & Kalko 2004; Valentin-Silva & Vieira 2015) and Paleotropical (Devi *et al.* 2016a, 2018) species of this genus, as well as vegetative propagation (Gartner 1989; Greig 1993; Lasso *et al.* 2009, 2012; Souza *et al.* 2009; Valentin-Silva & Vieira 2015). Valentin-Silva & Vieira (2015) addressed issues that link vegetative propagation and its contribution to the reproductive phenophases of two *Piper* species.

Reproductive phenology studies require adult individuals already capable of producing inflorescences. Fleming (1985) suggested as an inclusion criterion the sampling of individuals with a height of ≥ 1 m. However, this criterion is not suitable for all *Piper* species (see Valentin-Silva & Vieira 2015). The latter authors proposed the mandatory presence of reproductive structures (inflorescences with flower buds, flowers, or fruits; Fig. 1a) in individuals or inflorescence scars on branches (Fig. 1b), which indicates previous reproductive episodes. Thus, sampling of juvenile individuals can be avoided, which would bias the results.

The number of sampled individuals varies among phenological studies on *Piper* species. However, to facilitate the comparison of results between studies, some standardizations must be applied. When possible, at least 15 adult individuals of each species should be sampled in biweekly observations, which has been suggested as suitable for phenological studies (Morellato *et al.* 2010a). Monthly observation is not appropriate, as some phenophases may not be recorded in some species (see Mariot *et al.* 2003).

Standardization of the analyses is also important. Phenological data can be analyzed using activity and intensity indices (Morellato *et al.* 2010a), which allow evaluation of the period of occurrence of phenophases and their duration, in addition to other phenological parameters. The frequency and duration of phenophases can be classified according to Newstrom *et al.* (1994). Phenophases can be described using circular statistics (Morellato *et al.* 2010b) and their seasonality can be assessed using the Rayleigh test (Zar 2010). To test the potential effects of abiotic factors (*e.g.*, mean temperature, precipitation, and day length) on phenology, generalized linear models can be used for analyses (Crawley 2007).

Floral buds

Inflorescence production has been examined in a few studies, both on Neotropical (Marquis 1988; Mariot *et al.* 2003; Valentin-Silva & Vieira 2015; Valentin-Silva *et al.* 2018a) and Paleotropical (Devi *et al.* 2016a, 2018) species. Some Neotropical *Piper* species show latent flower buds (Marquis 1988; Valentin-Silva & Vieira 2015; Valentin-Silva *et al.* 2018a), *i.e.*, inflorescences are produced throughout the year, whereas anthesis of the flowers is restricted to a short period of the year, typically at the beginning of the rainy season. In addition, these species flower before those that do not have latent flower buds, and the duration of flowering is shorter, representing a possible escape mechanism from water stress (Valentin-Silva *et al.* 2018a). It is also possible that this temporal separation of the flowering period of these two species groups may reduce the competition for common pollinators. Due to the presence of latent flower buds, the separation of flowering into two phenophases (floral buds and flowers at anthesis) is important to consider avoiding errors in the calculation of phenological parameters (duration, concentration, start, and peak dates), in addition to not overestimating the period of availability of floral resources (pollen) to floral visitors.

Only two Paleotropical *Piper* species have been studied regarding phenology: *P. mullesua* Buch.-Ham. *ex* D.Don (Devi *et al.* 2016a) and *P. sylvaticum* Roxb. (Devi *et al.* 2018), both of which are dioecious. The respective authors recorded spike production throughout the year in both male and female *P. mullesua* and male *P. sylvaticum* plants. These results indicated that these species may have latent flower buds. However, this topic needs to be further explored in these and other Paleotropical *Piper* species, by observing whether they occur in both types of individuals (male and female) of dioecious species, as well as in inflorescences of monoecious species.

As some species with latent flower buds occur in different habitats (seasonal and aseasonal forests), it would be interesting to evaluate populations in these habitats to verify whether the production of latent inflorescences is an intrinsic characteristic of these species or a response to the environment. As an alternative option, greenhouse experiments could be conducted to evaluate the influence of water stress on the production of inflorescences and, consequently, on flowering (flowers at anthesis). According to Wright (1991), water stress can delay inflorescence production in *Piper* species; however, this study did not assess whether this effect also occurred in species with latent flower buds.

Flowers at anthesis

Flowering (flowers at anthesis) commonly occurs once per year (annual pattern *sensu* Newstrom *et al.* 1994), as observed in Neotropical

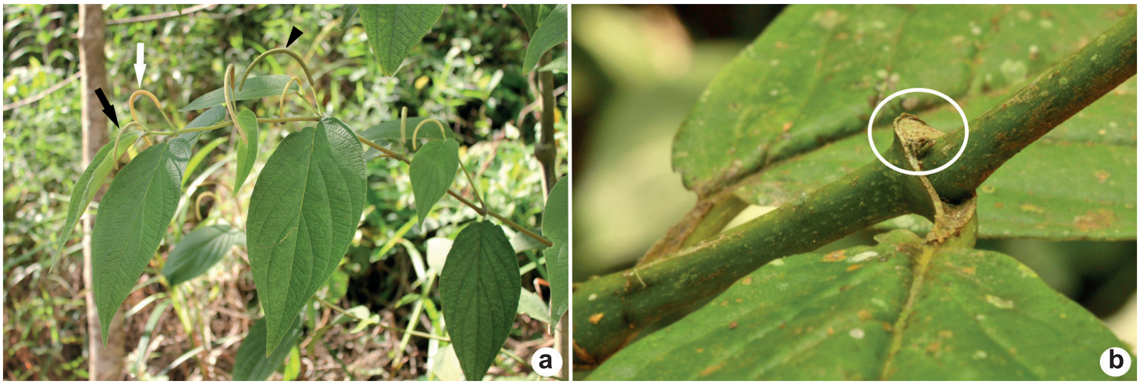

Figure 1 – a-b. Criteria for sampling adult *Piper* individuals – a. presence of reproductive structures; note spikes with floral buds (light green color; black arrow), flowers at anthesis (cream color; white arrow), and fruits (green color; arrowhead); b. presence of inflorescence scar on the branch (circle).

Piper species studied at different locations (Opler *et al.* 1980; Fleming 1985; Figueiredo & Sazima 2004; Thies & Kalko 2004; Valentin-Silva & Vieira 2015; Valentin-Silva *et al.* 2018a). When assessed at the community level, this phenophase typically occurs throughout the year (continuous pattern *sensu* Newtrom *et al.* 1994), as observed by Figueiredo & Sazima (2000) and Valentin-Silva *et al.* (2018a) in Brazil and by Thies & Kalko (2004) in Panama. This continuous pattern in the community is due to the different phenological patterns observed at the species level, such as annual, subannual, and continuous flowering (*sensu* Newstrom *et al.* 1994).

In Paleotropical species, an annual flowering pattern has also been observed at the species level (Devi *et al.* 2016a, 2018). However, the flowering peak can be simultaneous between male and female plants (Devi *et al.* 2016a) or sequential, with male plants flowering at a higher intensity before female plants (Devi *et al.* 2018).

Phenological patterns of species may differ between habitats. For example, Thies & Kalko (2004) observed that *Piper* species occurring in forest gaps tended to have longer flowering periods than species that occurred within the forest; in addition, the peak flowering period differed between habitats. Abiotic factors, such as climate, can also influence phenological patterns. Valentin-Silva *et al.* (2018a) showed that day length was positively correlated with the number of species flowering, as the flowering peak occurred during the rainy season when days are longer. This environmental variable is considered a trigger for flowering and is one of the most accurate predictors of this phenophase (Stevenson *et al.* 2008). This result corroborates the climatic hypothesis, which predicts that phenological activity is related to the seasonality of limiting environmental variables such as water and light availability (van Schaik *et al.* 1993; Fenner 1998).

Biotic factors such as pollinators can also influence phenological patterns. Fleming (1985) observed a temporal partition among five *Piper* species observed in Costa Rica, which can be interpreted as a mechanism to avoid or reduce competition for common pollinators and increase pollination effectiveness (competition hypothesis; van Schaik *et al.* 1993; Fenner 1998). By contrast, Valentin-Silva *et al.* (2018a) examined 17 species of *Piper* co-occurring in Brazil and found an overlap in the flowering period between species groups (*e.g.*, five of the eight species with latent flower buds flowered simultaneously at the beginning of the rainy season). As these species produce flowers with similar morphology, simultaneous flowering may attract more pollinators, thereby increasing pollination rates (facilitation hypothesis; van Schaik *et al.* 1993; Fenner 1998). Both competition and facilitation may be important in different areas, depending on pollinator availability. As these hypotheses are difficult to test in natural settings, the role of biotic vectors as modulators of plant phenology can be evaluated using the null model analysis (see Staggemeier *et al.* 2010).

The phylogenetic hypothesis predicting that closely related species tend to exhibit more similar phenological patterns than more distantly related species (Kochmer & Handel 1986) was tested on *Piper* species. However, Valentin-Silva *et al.* (2018a) found no association between phylogenetic relatedness and phenological patterns of the examined species; regardless, these authors suggested that the predominance of annual flowering frequency may be related to phylogenetic factors. Improving the phylogenetic resolution of species-rich clades, together with more phenological information, may thus provide new perspectives on how evolutionary history has affected the phenology of *Piper* species.

Fruiting

As with flowering, fruiting commonly follows an annual pattern at the species level (Opler *et al.* 1980; Fleming 1985; Marinho-Filho 1991; Thies & Kalko 2004; Valentin-Silva & Vieira 2015; Valentin-Silva *et al.* 2018a) and shows continuous pattern at the community level (Thies & Kalko 2004; Valentin-Silva *et al.* 2018a) in the Neotropics. In the Paleotropics, two *Piper* species showed a continuous pattern of fruiting (Devi *et al.* 2016a, 2018). Most of these studies did not separate data on immature and mature fruits due to the difficulty of recording ripe fruits in biweekly or even weekly observations (*e.g.*, Valentin-Silva & Vieira 2015), as these fruits remain on the plant for one or two days (Marquis 1988; Thies & Kalko 2004). Therefore, the fruiting period is long, which may be related to the low availability of ripe fruits per plant and night (Fleming 1981; Thies & Kalko 2004). Fleming (1981) observed that in *P. amalago* L., a few ripe fruits (1–3) were available per night over a period of 3–4 weeks. These analyses of ripe fruit availability and removal rate by dispersers were based on daily observations at night, as Neotropical *Piper* species are generally dispersed by frugivorous bats (Fleming 2004; Thies & Kalko 2004), mainly *Carollia perspicillata* (Linnaeus 1758) (Marinho-Filho 1991; Lima & Reis 2004). Further information on the dispersal ecology of Neotropical *Piper* species was compiled by Fleming (2004); however, the dispersal mechanisms of Paleotropical *Piper* species are still poorly understood.

Phenological patterns of fruiting can also differ between species, depending on the habitat in which they occur. Thies & Kalko (2004) observed fruiting in *Piper* species growing in a forest throughout the year, but with a staggered pattern among species. This pattern can be interpreted as a response to the limitation of dispersers, which helps reduce interspecific competition for dispersers in addition to reducing competition for germination sites. The authors also confirmed that *Piper* species occurring in forest gaps showed fruiting throughout the year, with each species showing more than one peak of fruit production and longer fruiting periods. The overlap of these long fruiting periods is associated with a broad spectrum of dispersers (bats, birds, and probably ants) and with the need for specific conditions for seedling establishment (gap formation).

Some of the hypotheses on factors influencing phenological patterns were also tested with respect to fruiting. Valentin-Silva *et al.* (2018a) showed that the number of species with fruits was positively correlated with mean temperature and day length of the months prior to the occurrence of the phenophase, and there was no phylogenetic structuring. Fruit production was constant throughout the year (continuous fruiting pattern), which is associated with the maintenance of frugivorous disperser populations (Snow 1965). These results indicate the importance of dispersers as modulators of the fruiting phenology of *Piper* species, as suggested by Thies & Kalko (2004).

Sexual expression

The sexual expression of *Piper* species is variable and tends to be related to the geographic distribution of the clades. Twenty-two species were analyzed (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.22626970.v1>). Neotropical species are considered to exclusively produce bisexual flowers (Jaramillo *et al.* 2008). However, functionally male flowers (staminate) have been observed in natural populations of four species, *i.e.*, *P. arboreum* Aubl., *P. caldense* C.DC., *P. cernuum* Vell., and *P. chimonanthifolium* Kunth (Figueiredo & Sazima 2000; Vargas-Rojas & Vieira 2017; Valentin-Silva *et al.* 2018b). Staminate flowers of these species showed cryptic unisexuality (flowers morphologically bisexual but functionally unisexual *sensu* Mayer & Charlesworth 1991).

Variations in the distribution of flowers on inflorescences were also reported by Valentin-Silva *et al.* (2018b). In *P. arboreum*, *P. caldense*, and *P. cernuum*, spikes with bisexual flowers and spikes with staminate flowers were observed. In addition to these types of inflorescences, *P. chimonanthifolium* showed spikes with bisexual and staminate flowers (mixed spikes), a characteristic described for the first time in a Neotropical *Piper* species. In all four species, the male spikes and the portion of mixed spikes with staminate flowers senesced after pollen release. Moreover, the distribution of inflorescence types varied between individuals of these four species, which directly influences their sexual expression (Valentin-Silva *et al.* 2018b). *Piper cernuum* was considered andromonoecious, whereas the populations of *P. arboreum* and *P. chimonanthifolium* appeared to be in transition to this type of sexual expression, as they are andromonoecious and hermaphrodite individuals. *Piper caldense* is probably androdioecious because individuals have hermaphrodite and male functions. Androdioecy is rare in angiosperms (Pannell 2002), and studies on other populations of this species may help answer this question.

A further interesting characteristic of *P. arboreum*, *P. caldense*, *P. cernuum*, and *P. chimonanthifolium* is variation in pistil length and in the size of spikes with bisexual and staminate flowers, indicating sexual dimorphism, as observed by Valentin-Silva *et al.* (2018b). The authors suggested that inflorescence length may be a diagnostic characteristic to identify the types of individuals in Neotropical *Piper* species that show sexual expression different from hermaphroditism. Because of the small size of flowers, analysis of floral morphology related to the functionality of flowers during anthesis is essential to determine the sexual expression of Neotropical *Piper* species. It is likely that studies of this type in other populations in the Neotropics will reveal further species with functionally unisexual flowers.

In the Paleotropics, *Piper* species with unisexual flowers and dioecy are predominant (Wanke *et al.* 2007; Jaramillo *et al.* 2008). In the Asian tropics, there are some species with bisexual flowers, such as *Piper longum* L. (Kanimozhi &

Sujatha 2015), and in the South Pacific, some species are monoecious (Jaramillo *et al.* 2008). Despite this, Ollerton (1996) noted in *P. novae-hollandiae*, an Australian species usually described as monoecious, individuals that only had spikes with staminate flowers. Female inflorescences tend to be shorter than those of males in some Paleotropical *Piper* species (Kanimozhi & Sujatha 2015; Devi *et al.* 2016b), indicating sexual dimorphism, similar to Neotropical species that have bisexual and staminate flowers.

Mixed inflorescences were observed in three dioecious species. *Piper pedicellatum* C.DC. has some inflorescences with bisexual and pistillate flowers in addition to female inflorescences (Lei & Liang 1998). *Piper sylvaticum* has some inflorescences with bisexual and staminate flowers in addition to male inflorescences (Devi *et al.* 2016b). In *Piper mullesua*, a few pistillate flowers have been observed along with staminate flowers in addition to male inflorescences (Devi *et al.* 2016b). However, these studies did not examine potential differences in length between these types of inflorescences. It would thus be interesting to analyze these variations in other populations, preferably under natural settings (Devi *et al.* 2016b studied cultivated individuals), or even in herbarium material (see Valentin-Silva *et al.* 2018b) to confirm such changes in the sexual expression in these species, considering that sexual expression can vary in time and space (Sakai & Weller 1999).

Floral biology

The minute flowers of *Piper* appear, at first glance, morphologically similar; both bisexual and unisexual flowers are perianthless and are protected by a bract, with 1–10 stamens and 3–4 carpels (Jaramillo & Manos 2001). However, there are variations regarding flower (relative size of filament and anther, orientation of the anther opening, presence or absence of pedicel) and inflorescence (packaging of flowers, position, length, presentation, color, and arrangement) (Jaramillo & Manos 2001). Studies involving aspects of floral biology were carried out with 29 species.

In bisexual flowers, floral events (pollen release and stigmatic exposure) are usually separated by time, characterizing dichogamy. Most *Piper* species show complete or incomplete protogyny (Figueiredo & Sazima 2000; Valentin-Silva *et al.* 2015, 2018c; Vargas-Rojas & Vieira 2017), however, there are reports of incomplete protandry (Figueiredo & Sazima 2000; Kikuchi *et al.* 2007) and adichogamy (Figueiredo & Sazima 2000). Apart from adichogamy, these reproductive mechanisms favor xenogamy. Despite this, autogamy or geitonogamy may occur in self-compatible species when an overlap between the pistillate and staminate phases of the flower occurs (Lloyd & Schoen 1992).

As most *Piper* species are protogynous, anthesis begins with the exposure of stigmas, which occurs sequentially and gradually and in a basipetal direction (Valentin-Silva *et al.* 2015, 2018c; Vargas-Rojas & Vieira 2017). This mode of stigmatic papillae exposure is related to both incomplete protogyny and stigma longevity (4–16 days; Valentin-Silva *et al.* 2018c), which increases the likelihood for stigmas to receive sufficient pollen grains (Cruden 2000). Valentin-Silva *et al.* (2018c) observed this trait in Neotropical *Piper* species with three and four stigmas, indicating that the mode of stigmatic papillae exposure was independent of the number of carpels in the flower.

Pollen release, in turn, is asynchronous and sequential, as it occurs in one stamen at a time, typically between 10:00 am and 2:00 pm, showing clump formation on the anther (Valentin-Silva *et al.* 2015, 2018c; Vargas-Rojas & Vieira 2017). This pattern differs from that of androecium development, which is asynchronous and occurs in a specific sequence. The lateral pairs of stamens develop simultaneously, and the median pair develops sequentially, with the median-anterior stamen being formed before the median-posterior stamen (Tucker 1982). During anthesis, pairs of lateral stamens release pollen at different times on the same day or on subsequent days; the median pair of stamens releases pollen sequentially on subsequent days (Valentin-Silva *et al.* 2015, 2018c). This trait was observed in Neotropical *Piper* species with two, three, four, and six stamens. Therefore, it does not depend on the number of stamens in the flower, although in flowers with more stamens, the period of pollen supply tends to be longer, increasing the likelihood of cross-pollination (Valentin-Silva *et al.* 2018c). Asynchronous and sequential pollen release has also been recorded in the staminate flowers of Neotropical species (Vargas-Rojas & Vieira 2017; Valentin-Silva *et al.* 2018c).

Based on the similarities between bisexual and unisexual flowers regarding morphology, floral development (Tucker 1982; Lei & Liang 1998; Jaramillo *et al.* 2008), and sequence of pollen release (Vargas-Rojas & Vieira 2017; Valentin-Silva *et al.* 2018c), in addition to the long-lived stigmas in *P. nigrum* (Menon 1949; Martin & Gregory 1962), a genus-wide pattern in the dynamics of floral events may exist. However, further studies on Paleotropical *Piper* species are needed to test this hypothesis. Studies on the floral biology of Paleotropical species generally examined the timing of pollen release and viability, in addition to stigmatic receptivity (Kanimozhi & Sujatha 2015; Chen *et al.* 2018), but do not explain how this dynamic occurs. However, Chen *et al.* (2018) studied the stigmatic receptivity of ten cultivars of *P. nigrum* at three anthesis stages using Peroxtesmo KO (Machery-Nagel, Düren, Germany). From the images of this study, it is possible to observe that the stigmatic papillae become receptive sequentially, gradually, and in a basipetal direction, which reinforces the suggested similarity with Neotropical species.

Piper flowers have only pollen as a resource and generally have a sweet or citrusy odor, as reported for 13 Neotropical species (Figueiredo & Sazima 2000) and two Australian species (Ollerton 1996). These odors may be related to the attraction of pollinators, which is one of the key functions of volatile organic compounds (Farré-Armengol *et al.* 2013). However, studies to elucidate the chemical composition of these odors and their role in attracting pollinators are scarce. Machado *et al.* (2021) observed that linalool compounds were predominant in the flowers of *P. mollicomum* Kunth, and their emission was correlated with a higher frequency of bee visits.

Pollination and mating systems

Thirty-six *Piper* species had floral visitors and pollinators evaluated (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.22626970.v1>). Neotropical *Piper* species are entomophilous and are pollinated by different species of bees, flies, and beetles (Tab. 1). Therefore, they are generalists in terms of ecology (number of pollinator species *sensu* Ollerton *et al.* 2007) and functionality (taxonomic diversity of pollinators *sensu* Ollerton *et al.* 2007). Other floral visitors have also been recorded, such as butterflies, wasps, hemipterans, and spiders (Fleming 1985; Figueiredo & Sazima 2000, 2004; Figueiredo 2003; Valentin-Silva *et al.* 2021). However, they were not considered pollinators because of their low abundance, their behavior and frequency of visits, and/or the absence of pollen adhering to the body.

Neotropical *Piper* flowers are typically visited during the day, with a peak in the late morning, mainly between 10:00 am and 11:00 am (Kikuchi *et al.* 2007; Vargas-Rojas & Vieira 2017; Valentin-Silva *et al.* 2021). However, there may be some variations in the peak visiting periods between *Piper* species (Thomazini & Thomazini 2002; Figueiredo 2003). Visitations by these insects can be seasonal, as their proportions of visits vary throughout the year (Fleming 1985; Thomazini & Thomazini 2002; Wisniewski *et al.* 2019). Insects generally exhibit similar visiting behavior, crawling along a part or over the full length of the inflorescence, and they commonly visit more than one inflorescence per plant (Figueiredo & Sazima 2000; Kikuchi *et al.* 2007; Wisniewski *et al.* 2019; Valentin-Silva *et al.* 2021). However, the duration of visits varies between insects. Bees and flies tend to show shorter visitation times than beetles, which can remain on the inflorescences for up to an hour, sometimes with little movement (Figueiredo & Sazima 2000; Figueiredo 2003; Wisniewski *et al.* 2019; Valentin-Silva *et al.* 2021).

The visiting behavior of such insects (bees, flies, and beetles) can affect the rates of autogamy and geitonogamy (Lloyd & Schoen 1992) in self-compatible *Piper* species. In the Neotropics, both self-compatible (13 species; Marquis 1988; Figueiredo & Sazima 2000; Kikuchi *et al.* 2007; Valentin-Silva *et al.* 2021) and self-incompatible species (16 species; Figueiredo & Sazima 2000; Vargas-Rojas & Vieira 2017; Valentin-Silva *et al.* 2021) have been reported. Figueiredo & Sazima (2000) and Valentin-Silva *et al.* (2021) studied seven common species, three of which showed divergent incompatibility systems between the examined populations. Considering that inter- and intraspecific variation in outcrossing rates is common (Barrett 2003), progeny analyses are required to confirm whether self-compatible *Piper* species are exclusively autogamous or whether they can benefit from the presence of pollinators.

Despite pollination by different insects, no studies have examined whether pollinators differ in terms of effectiveness in pollinating *Piper* species. Such studies could be performed on self-incompatible *Piper* species because of the difficulty in emasculating the flowers and isolating the effect of self-fertilization. Thus, it is possible to assess whether pollinators differ in terms of their contribution to the sexual reproduction of these plants.

Table 1 – Studies carried out on the pollinators of Neotropical *Piper* species.

Reference	Country	*Piper* species	Pollinators order (family/subfamily)	Pollinator species
Semple (1974)	Costa Rica	5	Coleoptera	7
			Hymenoptera (Apidae/Apinae, Halictinae)	1
Fleming (1985)	Costa Rica	4	Diptera (Syrphidae)	12
			Hymenoptera (Apidae/Apinae, Halictinae, Megachilinae)	14
Thomazini & Thomazini (2002)	Brazil	1	Hymenoptera (Apidae/Apinae, Colletinae, Halictinae)	20
Figueiredo & Sazima (2004)	Brazil	12	Coleoptera (Chrysomelidae, Scarabaeidae)	3
			Diptera (Calliphoridae, Lauxaniidae, Muscidae, Syrphidae)	49
			Hymenoptera (Apidae/Andreninae, Apinae, Colletinae, Halictinae)	22
Kikuchi *et al.* (2007)	Panama	1	Diptera (Syrphidae)	-
			Hymenoptera (Apidae/Apinae, Halictinae, Megachilinae)	8*
Vargas-Rojas & Vieira (2017)	Brazil	1	Diptera (Syrphidae)	7
			Hymenoptera (Apidae/Apinae)	8
Wisniewski *et al.* (2019)	Puerto Rico	4	Coleoptera (Curculionidae)	1
			Diptera (Drosophilidae, Heleomyzidae, Phoridae, Syrphidae)	10
			Hymenoptera (Apidae/Apinae)	1
Valentin-Silva *et al.* (2021)	Brazil	17	Coleoptera (Chrysomelidae, Curculionidae)	8
			Diptera (Stratiomyidae, Syrphidae)	13
			Hymenoptera (Apidae/Apinae, Colletinae, Halictinae, Megachilinae)	24

* = Halictinae species were not identified, as well as those of Syrphidae.

In addition to biotic pollinators, wind pollination has been reported in conjunction with insects (ambophily; Figueiredo & Sazima 2000). The occurrence of anemophily in *Piper* species is still controversial. Culley *et al.* (2002) reviewed the origin of anemophily in angiosperms. Even considering that anemophilous species do not consistently possess all characteristics associated with this pollination syndrome, Piperaceae did not appear to be wind-pollinated. Some studies have ruled out this pollination mechanism due to the formation of pollen clumps on the anther, possibly indicating the presence of pollenkitt (Semple 1974; Valentin-Silva *et al.* 2021). According to these studies, such pollen clumps can remain on the anther from one day to the next, even after rainfall or wind. By contrast, Figueiredo & Sazima (2000) observed powdery pollen in Neotropical *Piper* species. Despite this divergence, other characteristics indicate better suitability of *Piper* flowers for entomophily: abundant insect visitation in most species and stigmas closely surrounded by stamens (Valentin-Silva *et al.* 2021). An experiment to simulate the removal of pollen from anthers by the wind showed that when pollen is transported by wind, the distance traveled (up to 30 cm) is insufficient for cross-pollination to occur (Valentin-Silva *et al.* 2021). A respective study on *Piper* species producing powdery pollen may elucidate the importance of wind as a pollen vector in the sexual reproduction of these plants.

Valentin-Silva *et al.* (2021) evaluated the role of pollinators in the diversification of floral traits of Neotropical *Piper* species, and no correlation between the flower morphological characteristics and their pollinators was found, indicating phenotypic generalization. The authors suggest that dispersers which tend to be more specialized than pollinators of *Piper* may have influenced the diversification of the genus; however, further research is required.

The pollination biology of Paleotropical *Piper* species has been poorly studied (see Sen & Rengaian 2022), even though these species have predominantly unisexual flowers and probably depend on pollen vectors. The few existing studies were carried out mainly with *P. nigrum*, species originating in India that is widely cultivated throughout the humid tropics (Greig 2004). Spring tails (Collembola) were observed to visit the flowers in populations of four varieties of *P. nigrum* cultivated in Puerto Rico (Martin & Gregory 1962). However, as these insects are wingless, they likely contribute little to pollen flow between plants. Some authors proposed that water and wind may be important pollen vectors for sexual reproduction of black pepper (Menon 1949; Gentry 1955a,b), however, there is no experimental evidence (see Martin & Gregory 1962; Sasikumar *et al.* 1992). This species, which comprises several varieties that can be hermaphroditic, dioecious, or monoecious (Menon 1949), is self-pollinating or even apomictic (Gentry 1955b; Sasikumar *et al.* 1992; but see Pooja *et al.* 2022), both characteristics can be adaptations to cultivation (Martin & Gregory 1962). However, the occurrence of apomixis needs to be confirmed through an embryological study, which could also be performed on Neotropical *Piper* species with a high fruiting rate and low visitation frequency, such as *P. umbellatum* L. (Figueiredo & Sazima 2000; Valentin-Silva *et al.* 2021).

In addition to studies on *P. nigrum*, there are only two other studies on the aspects of pollination with Paleotropical *Piper* species. Ollerton (1996) observed that in Australia, flies (gall midges; Diptera: Cecidomyiidae) visit and lay eggs on male inflorescences of *P. novae-hollandiae* Miq., which produces sweet-smelling flowers. However, as no female inflorescences were observed, whether these flies contribute to pollen flow between plants is not yet known. An interesting floral visitor was observed by Okuyama (2014) in the Philippines, a crab species was found on male inflorescences of an unidentified *Piper* species. Although the author recorded the presence of anthers attached to the body of this crustacean, the absence of visits to female inflorescences and the record of this crab in only one individual of *Piper* indicates that this animal probably contributes little to pollen flow between plants.

Conclusion

The reproductive biology of *Piper* has advanced in recent years, mostly in Neotropical species. Some patterns can be observed, such as the predominance of annual flowering and fruiting, dichogamy (generally incomplete protogyny) with gradual and sequential exposure of stigmas, asynchronous pollen release, and pollination by insects. However, these aspects have not been extensively studied in the Paleotropical *Piper* species, and further studies are required to obtain basic information on the reproductive biology of these plants. From this, comparisons with Neotropical species can be made, allowing the verification of patterns in this genus. It will also be possible to apply these results to evolutionary studies, for example, regarding floral diversification.

From existing knowledge, it is possible to point out some gaps that deserve attention. Phenological data can be associated with germination ecology to assess their influence on reproductive success, especially for seasonal vegetation. Phenological responses can also be studied in the context of climate change. For example, the production of flower buds (latent and non-latent) in a scenario of lower precipitation and the consequences for subsequent phenophases and population dynamics. Another interesting point to be evaluated is the frequency of occurrence of cryptic unisexuality in morphologically bisexual flowers, considering that hermaphroditism is a typical characteristic of the Neotropical clade, and the selective pressures that can culminate in changes in the sexual expression of these plants. Regarding floral biology, nothing is known about the dynamics of floral odor release or the plant tissues that produce it. Chemical ecology studies can assess when the release of volatile organic compounds occurs, considering the predominance of dichogamy in Neotropical species and unisexual flowers in Paleotropical species. Moreover, fractions of these floral odors can be used in bioassays that evaluate their role in attracting different pollinators in a generalist pollination system such as *Piper*. Genetic analyses in self-compatible *Piper* species can contribute to studies on the evolution of mixed mating systems. Due to the organization of inflorescences and the visiting behavior of pollinators, the occurrence of this type of mating system may not be related to the unpredictability of pollinators, as commonly reported in the literature.

Piperaceae is a mega-diverse (approximately 3,500 species) and early diverging lineage of angiosperms. Besides *Piper*, there are four other genera in the family (*Manekia*, *Peperomia*, *Verhuellia*, and *Zippelia*) that have been little studied in relation to their reproductive biology. Information on these plants can be useful for understanding the diversification of angiosperms. Thus, the study of different aspects of the reproductive biology of *Piper* remains a promising field of research.

Acknowledgments

I thank the National Council for Scientific and Technological Development (CNPq) for the scientific initiation and Master's scholarships and the Coordination for the Improvement of Higher Education Personnel (CAPES) for the doctoral and postdoctoral scholarships facilitating different works using *Piper* as a study model.

References

Angulo-Sandoval P & Aide TM (2000) Leaf phenology and leaf damage of saplings in the Luquillo Experimental Forest, Puerto Rico. Biotropica 32: 415-422.

Asmarayani R (2018) Phylogenetic relationships in Malesian-Pacific *Piper* (Piperaceae) and their implications for systematics. Taxon 67: 693-724.

Barrett SCH (2003) Mating strategies in flowering plants: the outcrossing-selfing paradigm and beyond. Philosophical Transactions of the Royal Society B 358: 991-1004.

Chen YS, Dayod M & Tawan CS (2018) Anther dehiscence, pollen viability and stigma receptivity study on cultivars of black pepper (*Piper nigrum* L.). Pertanika Journal of Tropical Agricultural Science 41: 801-814.

Crawley MJ (2007) The R book. John Wiley & Sons, Chichester. 942p.

Cruden RW (2000) Pollen grains: why so many? Plant Systematics and Evolution 222: 143-165.

Culley TM, Weller SG & Sakai AK (2002) The evolution of wind pollination in angiosperms. Trends in Ecology and Evolution 17: 361-369.

Devi WD, Gajurel PR & Rethy P (2016a) Phenology of *Piper mullesua* Buchanan-Hamilton *ex* D. Don (Piperaceae) – a medicinally important dioecious plant. Pleione 10: 239-247.

Devi WD, Gajurel PR & Rethy P (2016b) Bisexuality in dioecious male plant: an unusual phenomenon of sex expression in *Piper* species. International Journal of Plant Reproductive Biology 8: 82-86.

Devi WD, Gajurel PR & Rethy P (2018) Phenological behavior of *Piper sylvaticum* Roxb. (Piperaceae), a medicinally useful species occurring in Eastern Himalayan region. International Journal of Plant Reproductive Biology 10: 84-89.

Di Stasi LC, Hiruma-Lima CA, Mariot A, Portilho WG & Reis MS (2002) Piperales medicinais. *In*: Di Stasi LC & Hiruma-Lima CA (eds.) Plantas medicinais na Amazônia e na Mata Atlântica. Ed. Unesp, São Paulo. Pp. 120-138.

Dyer L, Richards J & Dodson C (2004) Isolations, synthesis, and evolutionary ecology of *Piper* amides. *In*: Dyer LA & Palmer ADN (eds.) *Piper*: a model genus for studies of phytochemistry, ecology, and evolution. Kluwer Academic/Plenum Publishers, New York. Pp. 117-139.

Farré-Armengol G, Filella I, Llusia J & Peñuelas J (2013) Floral volatile organic compounds: between attraction and deterrence of visitors under global change. Perspectives in Plant Ecology, Evolution and Systematics 15: 56-67.

Fenner M (1998) The phenology of growth and reproduction in plants. Perspectives in Plant Ecology, Evolution and Systematics 1: 78-91.

Figueiredo RA (2003) Coleta de pólen, interações agonísticas e horários de atividade dos visitantes florais (Insecta: Diptera, Hymenoptera) de pimenteiras silvestres (Piperaceae). Revista de Etologia 5: 3-13.

Figueiredo RA & Sazima M (2000) Pollination biology of Piperaceae species in southeastern Brazil. Annals of Botany 85: 455-460.

Figueiredo RA & Sazima M (2004) Pollination ecology and resource partitioning in neotropical *Pipers*. *In*: Dyer LA & Palmer ADN (eds.) *Piper*: a model genus for studies of phytochemistry, ecology, and evolution. Kluwer Academic/Plenum Publishers, New York. Pp. 33-57.

Fleming TH (1981) Fecundity, fruiting pattern, and seed dispersal in *Piper amalago* (Piperaceae), a bat-dispersed tropical shrub. Oecologia 51: 42-46.

Fleming TH (1985) Coexistence of five sympatric *Piper* (Piperaceae) species in a tropical dry forest. Ecology 66: 688-700.

Fleming TH (2004) Dispersal ecology of Neotropical *Piper* shrubs and treelets. *In*: Dyer LA & Palmer ADN (eds.) *Piper*: a model genus for studies of phytochemistry, ecology, and evolution. Kluwer Academic/Plenum Publishers, New York. Pp. 58-77.

Gartner BL (1989) Breakage and regrowth of *Piper* species in rain forest understory. Biotropica 21: 303-307.

Gentry HS (1955a) Introducing black pepper into America. Economic Botany 9: 256-268.

Gentry HS (1955b) Apomixis in black pepper and jojoba? Journal of Heredity 46: 8.

Greig N (1993) Regeneration mode in neotropical *Piper*: habitat and species comparisons. Ecology 74: 2125-2135.

Greig N (2004) Introduction. *In*: Dyer LA & Palmer ADN (eds.) *Piper*: a model genus for studies of phytochemistry, ecology, and evolution. Kluwer Academic/Plenum Publishers, New York. Pp. 1-4.

Hartshorn GS & Hammel BE (1994) Vegetation types and floristic patterns. *In*: McDade LA, Bawa KS, Hespenheide HA & Hartshorn GS (eds.) La Selva: ecology and natural history of a neotropical rain forest. The University of Chicago Press, Chicago. Pp 73-89.

Jaramillo MA & Manos PS (2001) Phylogeny and patterns of floral diversity in the genus *Piper* (Piperaceae). American Journal of Botany 88: 706-716.

Jaramillo MA, Callejas R, Davidson C, Smith JF, Stevens AC & Tepe EJ (2008) A phylogeny of the tropical genus *Piper* using ITS and the chloroplast intron *psbJ-petA*. Systematic Botany 33: 647-660.

Kanimozhi K & Sujatha VS (2015) Reproductive biology of *Piper longum* L. Journal of Tropical Agriculture, 53: 206-212.

Kikuchi DW, Lasso E, Dalling JW & Nur N (2007) Pollinators and pollen dispersal of *Piper dilatatum* (Piperaceae) on Barro Colorado Island, Panama. Journal of Tropical Ecology 23: 603-606.

Kochmer JP & Handel SN (1986) Constraints and competition in the evolution of flowering phenology. Ecological Monographs 56: 303-325.

Lasso E, Engelbrecht BMJ & Dalling JW (2009) When sex is not enough: ecological correlates of resprouting capacity in congeneric tropical forest shrubs. Oecologia 161: 43-56.

Lasso E, Dalling JW & Bermingham E (2012) Tropical understory *Piper* shrubs maintain high levels of genotypic diversity despite frequent asexual recruitment. Biotropica 44: 35-43.

Lei LG & Liang HX (1998) Floral development of dioecious species and trends of floral evolution in *Piper sensu lato*. Botanical Journal of the Linnean Society 127: 225-237.

Letourneau DK (2004) Mutualism, antiherbivore, and trophic cascades: *Piper* ant-plants as a mesocosm for experimentation. *In*: Dyer LA & Palmer ADN (eds.) *Piper*: a model genus for studies of phytochemistry, ecology, and evolution. Kluwer Academic/Plenum Publishers, New York. Pp. 5-32.

Lima IP & Reis NR (2004) The availability of Piperaceae and the search for this resource by *Carollia perspicillata* (Linnaeus) (Chiroptera, Phyllostomidae, Carolliinae) in the Parque Municipal Arthur Thomas, Londrina, Paraná, Brazil. Revista Brasileira de Zoologia 21: 371-377.

Lloyd DG & Schoen DJ (1992) Self- and cross-fertilization in plants. I. Functional dimensions. International Journal of Plant Sciences 153: 358-369.

Machado DB, Ramos YJ, Queiroz GA, Defaveri ACA, Gobatto AA & Moreira DL (2021) Study of volatile chemical constituents and insect-plant interaction in *Piper mollicomum* Kunth (Piperaceae) from Tijuca Forest, Rio de Janeiro – RJ, Brazil. Revista Virtual de Química 13: 1216-1225.

Marinho-Filho JS (1991) The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. Journal of Tropical Ecology 7: 59-67.

Mariot A, Mantovani A & Reis MS (2003) Uso e conservação de *Piper cernuum* Vell. (Piperaceae) na Mata Atlântica: I. Fenologia reprodutiva e dispersão de sementes. Revista Brasileira de Plantas Medicinais 5: 1-10.

Marquis RJ (1988) Phenological variation in the neotropical understory shrub *Piper arieianum*: causes and consequences. Ecology 69: 1552-1565.

Martin FW & Gregory LE (1962) Mode of pollination and factors affecting fruit set in *Piper nigrum* L. in Puerto Rico. Crop Science 2: 295-299.

Mayer SS & Charlesworth D (1991) Cryptic dioecy in flowering plants. Trends in Ecology and Evolution 6: 320-325.

Menon KK (1949) The survey of *pollu* and root diseases of pepper. Indian Journal of Agricultural Science 19: 89-136.

Morellato LPC, Camargo MGG, d'Eça-Neves FF, Luize BG, Mantavoni A & Hudson IL (2010a) The influence of sampling method, sample size, and frequency of observations on plant phenological patterns and interpretation in tropical forest trees. *In*: Hudson IL & Keatley MR (eds.) Phenological research: methods for environmental and climate change analysis. Springer, Dordrecht. Pp. 99-121.

Morellato LPC, Alberti LF & Hudson IL (2010b) Applications of circular statistics in plant phenology: a case studies approach. *In*: Hudson IL & Keatley MR (eds.) Phenological research: methods for environmental and climate change analysis. Springer, Dordrecht. Pp. 339-359.

Newstrom LE, Frankie GW & Bake HG (1994) A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. Biotropica 26: 141-159.

Okuyama Y (2014) Repeated visitation by a sesarmid crab to male inflorescences of *Piper* sp. Bulletin of the National Museum of Nature and Science, Series B 40: 119-123.

Ollerton J (1996) Interactions between gall midges (Diptera: Cecidomyiidae) and inflorescences of *Piper novae-hollandiae* (Piperaceae) in Australia. The Entomologist 115: 181-184.

Ollerton J, Killick A, Lamborn E, Watts S & Whiston M (2007) Multiple meanings and modes: on the many ways to be a generalist flower. Taxon 56: 717-728.

Opler PA, Frankie GW & Baker HG (1980) Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 68: 167-188.

Pannell JR (2002) The evolution and maintenance of androdioecy. Annual Review of Ecology and Systematics 33: 397-425.

Pooja S, Sreekala GS & Vijaykumar BN (2022) Breeding system of fruit set in black pepper (*Piper nigrum* L.). The Pharma Innovation Journal 11: 1755-1759.

Sakai AK & Weller SG (1999) Gender and sexual dimorphism in flowering plants: a review of terminology, biogeographic patterns, ecological correlates, and phylogenetic approaches. *In*: Geber MA, Dawson TE & Delph LF (eds.) Gender and sexual dimorphism in flowering plants. Springer-Verlag, Berlin. Pp. 1-31.

Sasikumar B, George JK & Ravindran PN (1992) Breeding behaviour of black pepper. Indian Journal of Genetics and Plant Breeding 52: 17-21.

Semple KS (1974) Pollination in Piperaceae. Annals of the Missouri Botanical Garden 61: 868-871.

Sen S, Dayanandan S, Davis T, Ganesan R, Jagadish MR, Mathew PJ & Ravikanth G. (2019) Origin and evolution of the genus *Piper* in Peninsular India. Molecular Phylogenetics and Evolution 138: 102-113.

Sen S & Rengaian G (2022) A review on the ecology, evolution and conservation of *Piper* (Piperaceae) in India: future directions and opportunities. The Botanical Review 88: 333-358.

Simmonds SE, Smith JF, Davidson C & Buerki S (2021) Phylogenetics and comparative plastome genomics of two of the largest genera of angiosperms, *Piper* and *Peperomia* (Piperaceae). Molecular Phylogenetics and Evolution 163: 107229.

Snow DW (1965) A possible selective factor in the evolution of fruiting seasons in tropical forest. Oikos 15: 274-281.

Souza LA, Moscheta IS, Mourão KSM, Albiero ALM, Iwazaki MC, Oliveira JHG & Rosa SM (2009) Vegetative propagation in Piperaceae species. Brazilian Archives of Biology and Technology 52: 1357-1361.

Staggemeier VG, Diniz-Filho JAF & Morellato LPC (2010) The shared influence of phylogeny and ecology on the reproductive patterns of Myrteae (Myrtaceae). Journal of Ecology 98: 1409-1421.

Stevenson PR, Castellanos MC, Cortés AI & Link A (2008) Flowering patterns in a seasonal tropical lowland forest in western Amazonia. Biotropica 40: 559-567.

Thies W & Kalko EKV (2004) Phenology of neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). Oikos 104: 362-376.

Thomazini MJ & Thomazini APBW (2002) Diversidade de abelhas (Hymenoptera: Apoidea) em inflorescências de *Piper hispidinervum* (C.DC.). Neotropical Entomology 31: 27-34.

Tucker SC (1982) Inflorescence and flower development in the Piperaceae III. Floral ontogeny of *Piper*. American Journal of Botany 69: 1389-1401.

Valentin-Silva A & Vieira MF (2015) Phenology of two co-occurring *Piper* (Piperaceae) species in Brazil. Australian Journal of Botany 63: 581-589.

Valentin-Silva A, Coelho VPM, Ventrella MC & Vieira MF (2015) Timing of pollen release and stigma receptivity period of *Piper vicosanum* (Piperaceae): new insights into sexual reproduction of the genus. American Journal of Botany 102: 626-633.

Valentin-Silva A, Staggemeier VG, Batalha MA & Guimarães E (2018a) What factors can influence the reproductive phenology of Neotropical *Piper* species (Piperaceae) in a semi-deciduous seasonal forest? Botany 96: 675-684.

Valentin-Silva A, Batalha MA & Guimarães E (2018b) Neotropical *Piper* species: are they all hermaphroditic? Flora 244-245**:** 8-14.

Valentin-Silva A, Batalha MA & Guimarães E (2018c) Dynamics of pollen release and stigmatic exposure in Neotropical *Piper* species: a possible pattern for the genus. International Journal of Plant Sciences 179: 287-295.

Valentin-Silva A, Batalha MA & Guimarães E (2021) Disentangling the ecological basis of floral trait variation in Neotropical *Piper* species. Botanical Journal of the Linnean Society 195: 622-635.

van Schaik CP, Terborgh JW & Wright SJ (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annual Review of Ecology and Systematics 24: 353-377.

Vargas-Rojas DL & Vieira MF (2017) Sex expression, breeding system and pollinators of *Piper caldense* (Piperaceae) in the Brazilian Atlantic Forest. Acta Biológica Colombiana 22: 370-378.

Wanke S, Jaramillo MA, Borsch T, Samain MS, Quandt D & Neinhuis C (2007) Evolution of Piperales – *matK* gene and *trnK* intron sequence data reveal lineage specific resolution contrast. Molecular Phylogenetics and Evolution 42: 477-297.

Wisniewski C, Bornstein AJ & Wood DL (2019) Eating out or dining in: insect-plant interactions among species of *Piper* in the Rio Abajo Forest Preserve, Puerto Rico. Selbyana, 33: 1-15.

Wright SJ (1991) Seasonal drought and the phenology of understory shrubs in a tropical moist forest. Ecology 72: 1643-1657.

Zar JH (2010) Biostatistical analysis. Prentice-Hall, Upper Saddle River. 944p.

Area Editor: Dr. André Rech
Received on September 19, 2022. Accepted on December 21, 2022.