



Original article

When should fig fruit produce volatiles? Pattern in a ripening process

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ABSTRACT

Ripe fruit need to signal their presence to attract dispersal agents. Plants may employ visual and/or olfactory sensory channels to signal the presence of ripe fruit. Visual signals of ripe fruit have been extensively investigated. However, the volatile signatures of ripe fruit that use olfactorily-oriented dispersers have been scarcely investigated. Moreover, as in flowers, where floral scents are produced at times when pollinators are active (diurnal versus nocturnal), whether plants can modulate the olfactory signal to produce fruit odours when dispersers are active in the diel cycle is completely unknown. We investigated day–night differences in fruit odours in two species of figs, *Ficus racemosa* and *Ficus benghalensis*. The volatile bouquet of fruit of *F. racemosa* that are largely dispersed by bats and other mammals was dominated by fatty acid derivatives such as esters. In this species in which the ripe fig phase is very short, and where the figs drop off soon after ripening, there were no differences between day and night in fruit volatile signature. The volatile bouquet of fruit of *F. benghalensis* that has a long ripening period, however, and that remain attached to the tree for extended periods when ripe, showed an increase in fatty acid derivatives such as esters and of benzenoids such as benzaldehyde at night when they are dispersed by bats, and an elevation of sesquiterpenes during the day when they are dispersed by birds. For the first time we provide data that suggest that the volatile signal produced by fruit can show diel differences based on the activity period of the dispersal agent.

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1. Introduction

When fleshy fruit ripen, their seeds are ready for dispersal by fruit and seed dispersal agents. The ripening process varies, however, depending on whether the fruit is climacteric or not (Barry and Giovannoni, 2007; Defilippi et al., 2009). In climacteric fruit, the fruit odour characteristic of the ripened phase peaks sharply as a result of a rise in ethylene production, and a corresponding quick onset and completion of ripening. In non-climacteric fruit, there is no sharp rise in ethylene, gradual ripening, and therefore no peak in volatiles associated with the ripening process (Brady, 1987; Barry and Giovannoni, 2007). Climacteric fruit soften and become sweeter during the ripening phase during which there is also increased respiration and higher CO₂ production. Examples of climacteric fruit include banana, melon, and mango, while those of non-climacteric fruit include olives, cacao and strawberry (Janick, 2005). The climacteric nature of fruit has been extensively studied in fruit important in horticulture, since it is necessary to understand the ripening process in terms of optimum harvesting time and post-harvest shelf life. For example, there appears to be a general inverse

relationship between ethylene production and post-harvest life (Defilippi et al., 2009). Consequently, non-climacteric varieties of climacteric fruit have also been produced by plant breeders in order to increase the length of time fruit can be stored without spoilage. However, non-climacteric varieties have an altered fruit odour compared to the parental climacteric cultivars, e.g. non-climacteric melon cultivars have lower levels of total volatiles and lack volatile esters but have higher levels of aldehydes and alcohols (Shalit et al., 2001). Therefore, the climacteric nature of the fruit may determine the type of volatiles produced and thus the type of dispersal agent that is attracted to it (Borges et al., 2008). While the signal value of fruit colour for attracting particular dispersal agents has received considerable attention (e.g. Wheelwright and Janson, 1985; Siitari et al., 1999; Schmidt et al., 2004; Burns et al., 2009; Lomáscolo et al., 2010), the signal relevance of fruit odour has been scarcely investigated (Borges et al., 2008). Therefore while colour, size, shape, and nutrients within fruits have been usually considered as parameters characterising fruit dispersal syndromes (Gautier-Hion et al., 1985; Flörchinger et al., 2010), fruit odours have rarely been used in this characterisation (Borges et al., 2008).

There is virtually no knowledge of the climacteric nature of the wild relatives of cultivated fruit, or of any wild fruit, for that matter. Knowledge of the process of ripening is critical to an understanding of fleshy fruit, fruit ripening and seed dispersal since it could affect

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many aspects of dispersal ecology, e.g. the length of time dispersers may be attracted to the fruit, the type of dispersal agents attracted based on fruit odours produced, and the length of time developing seeds need to be protected on the plant itself, with important consequences for plant reproductive strategies. For example, fruit that ripen quickly may require lower investment in protective secondary metabolites compared to those that ripen slowly. This could also influence the nutritive value of fruit to dispersal agents. The edible portions of fruit that provide the attractive nutrient package for the dispersal agents may originate from varied tissues that range from the peduncle in edible figs, through the mesocarp in peach and the aril in mangosteen (Coombe, 1976). Therefore, knowledge of the tissues constituting the fruit could also be important in understanding the type of fruit pulp maturation process (Goulao and Oliveira, 2008) and consequently the type of fruit odour signal available to the dispersal agent. However, this remains completely uninvestigated. Furthermore, fruit are metabolically attached to the plant, and like flowers that have been shown to produce pollinator-attracting volatiles at times when the specific pollinators are most active (diurnal versus nocturnal pollinators) (Matile and Altenburger, 1988; Loughrin et al., 1990; Raguso et al., 2003; Raguso, 2008), fruit should also produce volatiles with a daily rhythm that matches the activity of their dispersal agents (nocturnal versus diurnal dispersers). This hypothesis has, however, never been investigated.

The only wild fruit whose ripening process has been investigated is the sacred fig *Ficus religiosa* (Galil et al., 1973). The syconium (fruit) of the sacred fig was found to be climacteric with a sharp peak in ethylene a few days before the pollinating fig wasps that are developing within the syconia enclose, mate within the fig, and leave the syconia with pollen to enter a pollen-receptive fig. The ethylene peak was matched by a respiratory increase and the onset of the softening process leading to syconium ripening to attract the seed dispersal agents (Galil et al., 1973). Work on the domesticated figs *Ficus sycomorus* and *Ficus carica* also seemed to indicate that all fig species produce climacteric fruit (Marei and Crane, 1971; Zeroni et al., 1976; Owino et al., 2006), which would imply a sharp peak in volatile production during syconium development and a rapid softening process. In this paper, however, we do not examine changes in volatile production through the entire development of the fig syconia. We investigate variation in diel production of volatile organic compounds by ripe figs in two fig species with different lengths of ripening phases, and attempt to relate these patterns to disperser identity and activity. We erect and test the hypothesis that, as in floral volatile attractants, volatile production in fruit which attract their dispersers by olfactory processes should be most pronounced when their dispersers are most active during the diel cycle. Since our data are limited, this must be considered as a preliminary test of the hypothesis.

2. Materials and methods

2.1. Natural history, species and study site

The fig syconium undergoes development in certain distinct phases based on interactions with their pollinating wasps which develop within the syconia. These periods are: pre-pollen receptive (A), pollen receptive (B), inter-floral and wasp development (C), wasp dispersal (D), and seed maturation (E) phases (Galil and Eisikowitch, 1968). The fruit ripening process can, therefore, only begin after the D phase once the pollinating fig wasps have left the syconia, since dispersal agents should not be attracted to the syconia before this time.

We captured E-phase fig volatiles of two species: *Ficus racemosa* L. (Section: *Sycomorus*; Subsection: *Sycomorus*) and *Ficus benghalensis*

L. (Section: *Urostigma*; Subsection: *Conosycea*) in the campus of the Indian Institute of Science, Bangalore, India (12° 58' N and 77° 35' E). *F. racemosa* is a tall free-standing tree with cauliflorous figs borne in large clusters on the main trunk and also on larger branches. *F. benghalensis* is a tall hemi-epiphytic fig with large aerial roots, and figs borne singly or in small axillary clusters among the leaves. The fruit of *F. racemosa* is dispersed largely by bats (Tang et al., 2007) and other mammals at night, while that of *F. benghalensis* is dispersed by birds during the day (Midya and Brahmachary, 1991) and bats at night (Goveas et al., 2006; R.M. Borges, pers. observ.). Ripe fruit of *F. racemosa* are yellowish-pink to red while those of *F. benghalensis* are bright red in colour. The E phase of *F. racemosa* is very short (3–4 days) with the figs dropping off rapidly, while that of *F. benghalensis* is much longer, up to 19 days (8.9 ± 4.5 days [mean \pm SD]; $n = 40$ tagged figs). Therefore, *F. racemosa* and *F. benghalensis* differ in ripening and these differences might therefore provide useful insights into the adaptive nature of volatile production patterns.

2.2. Fruit volatile collection and identification

Volatile organic compounds (VOCs) from E-phase fig syconia were collected by headspace adsorption techniques. Figs from each single tree were enclosed in a polyethylene terephthalate (Nalophan®) bag (Kalle Nalo GmbH, Wursthüllen, Germany) through which a constant air flow was maintained over an Alltech Super Q® volatile collection trap (VCT; ARS Inc., Gainesville, Florida) for 1 h per sample. Incoming air was cleaned using activated charcoal filters (Sigma-Aldrich). The same fig bunch was sampled in the day (1100 h) and at night (2300 h) in the case of *F. benghalensis*. However, for *F. racemosa* since ripe figs lose their connections to the stalks on handling, the same bunch could not be sampled at both times; instead a similar bunch adjacent to the bunch sampled in the day was sampled at night immediately on removal from the tree. Since syconia of *F. benghalensis* are axial, usually occurring in pairs surrounded by leaves, we included the leaves for the volatile extraction as well, since volatiles produced by them could also constitute part of the VOC signal. Furthermore, removal of leaves may initiate the production of wounding-related VOCs which is a common response in plants to vegetative tissue damage (Unsicker et al., 2009), and may interfere with the normal profile of VOCs produced. Therefore, terminal twigs containing syconia together with leaves were hermetically sealed in Nalophan bags (60 × 60 cm) for 1 h to let the volatiles accumulate inside the bag. Each bag was previously fitted with a sealed outlet for facilitating VOC collection. After 1 h, the VOCs accumulated inside the bag were passively collected using a SuperQ trap at a flow rate of 188 ml min⁻¹ controlled using a micropump (Aalborg Instruments, Orangeburg, NY, USA). The volatile collection bags contained 4–12 syconia along with 10–14 leaves. Therefore, in *F. benghalensis*, we considered fruit and leaves subtending them as the VOC production unit. We collected thirteen paired diurnal and nocturnal VOCs from six trees. In the case of *F. racemosa*, for each extraction, 20 E-phase syconia were collected from trees and VOCs were adsorbed on to VCTs using a dynamic headspace technique with 111 ml min⁻¹ as incoming and 94 ml min⁻¹ as outgoing air flow rates. Three such paired sets of extractions were done for *F. racemosa* from three trees, one pair per tree.

The VCTs were eluted with 150 µl of dichloromethane; the eluate was concentrated to 10 µl to which 0.5 µl of the internal standard cumene at a concentration of 200 ng ml⁻¹ was added. A quantity of 4 µl of this mixture was injected into a gas chromatography-mass spectrometry instrument (Agilent-HP GC model 6890N, MS model 5973N) operating in a split-less mode fitted with an HP-5MS column of 60 m length and 250 µm internal diameter with a 0.25 µm film thickness. Helium was used as the carrier gas at a flow rate of 1.5 ml min⁻¹. Optimal compound separation was achieved using the

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