



Floral scent in Annonaceae

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Many species of Annonaceae are known for their distinctive, penetrating floral aromas. Numerous pollination studies have documented floral scents which probably play a key role in specialized pollination strategies. In particular, floral scents appear to play crucial roles in deceptive pollination strategies, contributing to floral mimicry of ripe or decaying fruits, fungi and, potentially, carrion or faeces. Occasionally, floral scent may advertise genuine floral rewards, as is the case for two species of *Unonopsis* pollinated by male euglossine bees. To date, ten studies have chemically characterized floral scent for 24 species representing 11 genera of Annonaceae. In this review, I discuss the chemical composition and diversity of the analysed floral scents in Annonaceae. I also summarize and discuss a wide range of (human) perceptual descriptions of floral scent found throughout the literature on Annonaceae. I have framed discussions of floral scent in Annonaceae in ecological and evolutionary contexts whenever possible. © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2012, **169**, 262–279.

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INTRODUCTION

Flowers of Annonaceae are frequently noted to have strong, distinctive floral scents. Indeed, numerous studies have linked floral scent to specialized pollination syndromes in tropical Annonaceae. Although floral scent probably plays a key role in the reproductive ecology of many species of Annonaceae, relatively little work has been carried out to characterize scents within the family. This is not a shortcoming unique to Annonaceae research, however. A review by Knudsen *et al.* (2006) indicated that, at that time, the majority of angiosperm families had been subjected to little or no research on floral scent. Furthermore, studies of floral biology and pollination ecology, historically, have been biased towards visual aspects of floral phenotype, and most humans typically lack a reliable vocabulary with which to characterize odour and communicate its qualities (Raguso, 2008). Thus, characterizations of floral scent (or a lack thereof) are lacking from some studies focusing on floral biology or pollination ecology of Annonaceae, especially in work

from previous decades. At best, floral scents are referred to colloquially (e.g. Gottsberger, 1988; Gottsberger, Meinke & Porembski, 2011).

Existing floral scent characterizations in Annonaceae, whether by chemical analysis or human perception, show scent to be a dynamic and diverse component of floral phenotype, warranting increased attention as a crucial component of pollination ecology in the family. In this article, I briefly review (in the context of early diverging angiosperms and, in particular, Annonaceae) the ecological and evolutionary importance of floral scent, its utility as a phylogenetic trait and current methods for its analysis. I then present an overview of the existing literature on floral scents in Annonaceae and suggest directions in which this research is headed.

ECOLOGICAL AND EVOLUTIONARY ASPECTS OF FLORAL SCENT

The scent of a flower typically consists of a blend of volatile compounds emitted by floral tissues. Although floral scent is frequently studied as it relates to plant–pollinator interactions, the scent

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blend consists of volatiles acting as a 'signal' to other organisms in the environment (e.g. pollinators or herbivores) and volatiles which may represent by-products of biosynthetic pathways, neutral genetic variation or other environmental factors (Raguso, 2003). It is important to keep this in mind when considering ecological implications of complex floral scent blends, as is the case in most analysed species of Annonaceae. Certain scent compounds may be indicative of specialized pollination strategies, whereas other compounds may reflect phylogenetic constraints, plant defence or other evolutionary or ecological factors (Raguso, 2008; Junker & Blüthgen, 2010).

Studies of floral scent in early diverging angiosperms (angiosperms that belong to neither the monocots nor the eudicots) suggest that floral scent volatiles arose from compounds previously associated with plant defence (Pellmyr & Thien, 1986). Strong floral odours, with dull coloration, fleshy petals and, occasionally, thermogenesis, are traits common in extant lineages of these plants (Thien, Azuma & Kawano, 2000; Endress, 2010). These floral traits are typically linked to pollination by beetles and flies (Thien *et al.*, 2000; Silberbauer-Gottsberger, Gottsberger & Webber, 2003; Endress, 2010), and diverse families of Coleoptera and Diptera were already present when early angiosperms underwent rapid radiation and diversification (Baker & Hurd, 1968; Ren, 1998; Thien *et al.*, 2000). Thus, insect perception of and interaction with floral odour, colour and morphology are central to the rapid diversification of reproductive strategies seen within early diverging angiosperms (Thien *et al.*, 2000). The study of floral scent in the extant lineages (such as Annonaceae) provides a unique and important perspective on interactions between the earliest flowering plants and potential insect pollinators (Pellmyr & Thien, 1986; Jürgens, 2009). Floral scent is of particular interest in Annonaceae, as many species across multiple genera share a similar floral bauplan (van Heusden, 1992), but exhibit a fascinating diversity of floral scent and diverging pollination strategies (e.g. Silberbauer-Gottsberger *et al.*, 2003; Saunders, 2012).

If pollinators and herbivores exert strong selective pressures on floral volatile composition, we might expect floral scent to have low phylogenetic utility. Knudsen *et al.* (2006) reviewed 268 published papers on floral scent, concluding that, as a result of the high variability of floral scent composition between closely related individuals, floral scent is not particularly informative for the characterization of clades at or above the generic level. However, Knudsen *et al.* (2006) acknowledged that floral scent could provide a better fit to phylogenetic trees if particular biosynthetic scent pathways were to show notable

phylogenetic constraints within currently under- or unstudied families or genera (see Knudsen & Ståhl, 1994; Levin, McDade & Raguso, 2003). At lower taxonomic levels, several authors have found floral scent composition to be useful in the elucidation of ecological or evolutionary patterns, especially between closely related species and within or between populations (e.g. Knudsen, 1999; Levin, Raguso & McDade, 2001; Raguso *et al.*, 2003; Mant, Peakall & Schiestl, 2005; Majetic, Raguso & Ashman, 2008). In these studies, floral scent is linked to the pleiotropy of floral biochemistry, edaphic plasticity and potential incipient speciation, demonstrating the compelling role of floral scent in our understanding of floral ecology and evolution.

ANALYSIS AND CHARACTERIZATION OF FLORAL SCENT

When analysing floral scent, whether by human perception or by chemical analysis techniques, it is important to keep several factors in mind. Volatiles emitted from flowers may vary spatially (from different floral organs or locations within organs), temporally (with diurnal, nocturnal or circadian rhythms), between different stages of floral ontogeny, in association with post-pollination changes or through the process of senescence (Moorherjee, Trenkle & Wilson, 1990; Knudsen & Tollsten, 1991; Schade, Legge & Thompson, 2001; Flamini, Cioni & Morelli, 2003; Raguso *et al.*, 2003; Goodrich *et al.*, 2006). Flowers of Annonaceae are typically protogynous, exhibiting dichogamy in their transition from female to male sexual stage. Existing studies characterizing floral scent in Annonaceae, whether by chemical analyses or human perception alone, show scent to be a highly dynamic character with potential variation between female and male stages of floral ontogeny and/or a potential link to diurnal rhythms, especially when in combination with floral thermogenesis (Armstrong & Marsh, 1997; Nagamitsu & Inoue, 1997; Momose, Nagamitsu & Inoue, 1998a; Gottsberger, 1999; Jürgens, Webber & Gottsberger, 2000; Silberbauer-Gottsberger *et al.*, 2003; Webber & Gottsberger, 2003; Goodrich *et al.*, 2006; Ratnayake *et al.*, 2006, 2007; Teichert *et al.*, 2008; Goodrich & Raguso, 2009; Silva & Neta, 2010; Braun, Dötterl & Gottsberger, 2011). Thus, time of day and floral ontogenetic stage are important factors when making scent 'observations' for species of Annonaceae.

Flower scent should also be differentiated from vegetative scents, ambient environmental scents and scents caused by plant wounding, especially when sampling cut flowers. In chemical analyses of floral scent, vegetative and ambient control samples can be

used to distinguish between vegetative or ambient volatiles and floral volatiles. Some volatiles may be released from both floral and vegetative tissues, making it difficult to assess the importance of these volatiles in flower-specific functions of pollinator attraction and behavioural manipulation.

Some of the most common scent collection techniques for floral volatiles include static headspace collection using solid-phase microextraction (SPME) and varied forms of dynamic headspace collection. The SPME methods allow for rapid field and laboratory sampling and broad qualitative analysis of floral scent; however, only relative quantities of volatile compounds can be inferred from these methods, and these data are influenced by several factors in addition to the abundance of a compound in the sample. Dynamic headspace collection techniques generally require longer times for scent collection, except when small scent traps are used in combination with direct thermal desorption (see Dötterl & Jürgens, 2005). Dynamic headspace methods are not as practical for cut flowers or dissected floral organs because the volatiles emitted from dissected tissue after several hours may not represent the floral volatiles emitted under normal physiological conditions. Dynamic headspace sampling provides a more accurate quantification of volatiles emitted and, with the addition of internal and external standards, scent emission rates can be calculated. Furthermore, several subsamples of the eluate can be injected on different gas chromatography (GC) columns under different conditions, which is minimally necessary for the identification of unknown compounds. A more detailed explanation of the techniques and considerations for their use is given in Agelopoulos & Pickett (1998), Raguso & Pellmyr (1998), Flamini *et al.* (2003) and Tholl *et al.* (2006).

Detailed chemical analyses of floral scent are not always practical because of technological constraints and the time and/or funding necessary for such analyses. Floral scent characterization based on human perception alone can provide valuable preliminary information. Human perceptions of scent may vary somewhat between individuals, as discussed by Goodrich *et al.* (2006) with regard to the floral scent of *Asimina triloba* (L.) Dunal (a temperate species of Annonaceae). The floral scent of *A. triloba* has been characterized as stinking or unpleasant with specific reference to fermentation (Delpino, 1874), putatively derived from decomposing albuminoid or nitrogenous compounds (Kerner von Marilaum, 1895) or foetid, similar to decaying meat (Kral, 1960). Chemical analysis has shown that the floral scent of *A. triloba* contains many of the same fermentation products as emitted by baker's yeast (*Saccharomyces cerevisiae*), including acetic acid, ethyl acetate, ethanol, 3-methyl-

1-butanol, 3-hydroxy-2-butanone and butanediols (Goodrich *et al.*, 2006). However, the floral scent lacks nitrogen- or sulphur-containing compounds typical of decomposing meat or the odour of carrion-mimicking flowers (Kite & Hetterscheid, 1997; Stensmyr *et al.*, 2002; Jürgens, Dötterl & Meve, 2006).

Although descriptions, such as 'fermented' and 'yeasty', most accurately represent the chemical composition of *A. triloba* floral scent, all the descriptions listed above fall within a similar odour genre distinctly different from human perceptions of 'sweet', 'fruity' or 'pleasant'. The simple distinction between pleasant and unpleasant floral scents (based on human perception) may yield some information regarding pollination strategy. Common floral compounds, such as linalool, geraniol and phenylacetaldehyde, are perceived by humans as 'very pleasant' and 'sweet', and are known to be highly attractive to butterflies, moths and bees (Knudsen & Tollsten, 1993; Andersson *et al.*, 2002; Dobson, 2006). Common floral odours unpleasant to most humans may mimic scents of fermentation or protein decomposition, and these compounds (such as ethanol, indole or dimethyl disulphide) are more likely to attract saprophilous beetles and flies (Nout & Bartelt, 1998; Stensmyr *et al.*, 2002; Jürgens *et al.*, 2006). Further differentiation of floral odours, such as the distinction between 'sour, fermenting fruits' or 'foetid, decomposing carrion', may yield even more clues regarding distinct, if perhaps overlapping, pollinator fauna.

FLORAL SCENT CHEMISTRY AND POLLINATION IN ANNONACEAE

Flowers of Annonaceae commonly exhibit characters typical of early angiosperms, including protogyny, distinctive floral scents, fleshy petals, formation of a chamber and, occasionally, thermogenesis (Thien *et al.*, 2000; Silberbauer-Gottsberger *et al.*, 2003). Most species studied in Annonaceae are pollinated by beetles and exhibit characteristics typical of small or large beetle pollination syndromes, including fleshy petals or food bodies, fruity, spicy or decaying scents and the formation of protective chambers (Momose *et al.*, 1998b; Gottsberger, 1999; Silberbauer-Gottsberger *et al.*, 2003; Webber & Gottsberger, 2003). Although fly pollination is less common in the family (Willson & Schemske, 1980; Norman, Rice & Cochran, 1992; Su *et al.*, 2005), Silberbauer-Gottsberger *et al.* (2003) noted the occasional occurrence of characters consistent with this syndrome in Old and New World Annonaceae: spots of translucent tissue, unpleasant, sour or fermenting scents and nectar production. Thrips have been identified as either primary or

secondary pollinators in a few species of Annonaceae (Momose *et al.*, 1998a; Jürgens *et al.*, 2000; Norman, 2003; Silberbauer-Gottsberger *et al.*, 2003). In rare instances, male euglossine bees (Carvalho & Webber, 2000; Teichert *et al.*, 2008) or cockroaches (Nagamitsu & Inoue, 1997) have been identified as pollinators.

In many of the published pollination studies of Annonaceae, including those described above, distinctive floral scents are thought to be crucial components of pollinator attraction. Many floral volatile compounds identified in Annonaceae (Ma *et al.*, 1988; Jürgens *et al.*, 2000; Goodrich *et al.*, 2006; Ratnayake *et al.*, 2007; Teichert, 2008; Teichert *et al.*, 2008; Goodrich & Raguso, 2009; Braun *et al.*, 2011; Pripdeevech, 2011; Teichert, Dötterl & Gottsberger, 2011) have been shown in other studies to attract known pollinator fauna. For example, floral scents for a number of nitidulid beetle-pollinated species contain aliphatic esters and alcohols attractive to species of nitidulid beetles (Phelan & Lin, 1991; Bartelt & Wicklow, 1999; Peña *et al.*, 1999; Jürgens *et al.*, 2000). The floral scent of euglossine bee-pollinated *Unonopsis stipitata* Diels contains trans-carvone oxide, a compound shown in field bioassays to be highly attractive to male euglossine bees (Whitten *et al.*, 1986; Teichert *et al.*, 2008). Clearly, floral scent should be expected to play a key role in the reproductive biology of many species of Annonaceae.

To date, ten studies (Ma *et al.*, 1988; Jürgens *et al.*, 2000; Goodrich *et al.*, 2006; Ratnayake *et al.*, 2007; Teichert, 2008; Teichert *et al.*, 2008, 2011; Goodrich & Raguso, 2009; Braun *et al.*, 2011; Pripdeevech, 2011) have described floral scent compounds for 24 species of Annonaceae, representing 11 genera, in North and South America and South-East Asia (see Table 2). Compounds identified in these species can be divided into five major compound classes: aliphatics, aromatics (benzenoids), isoprenoids (terpenes), nitrogen-containing compounds and sulphur-containing compounds. These categorizations are based on chemical structure and a broad understanding of plant secondary metabolic pathways, as described by Knudsen *et al.* (2006). The diversity of compounds in each of these categories varies widely between species, as indicated in Table 2. The major compound classes identified in Annonaceae are common to most angiosperm families sampled thus far, with the exception of nitrogen- and sulphur-containing volatiles, which are typically rare (Knudsen *et al.*, 2006). However, the specific compounds produced and the predominance of certain compound classes over others in certain species may be more informative in an ecological or evolutionary context.

For example, all species included in the study of Jürgens *et al.* (2000) occurred in the Manaus region of Brazil, but are not closely related to one another

based on several morphological and molecular phylogenetic studies of the family (Doyle & Le Thomas, 1996; Richardson *et al.*, 2004; Couvreur *et al.*, 2008; Chatrou *et al.*, 2012). Five of the six species in this study [*Anaxagorea brevipes* Benth., *Anaxagorea dolichocarpa* Sprague & Sandwith, *Duguetia asterotricha* (Diels) R.E.Fr., *Rollinia insignis* R.E.Fr. (now *Annona neoinsignis* H.Rainer), *Xylopia aromatica* (Lam.) Mart. and *Xylopia benthamii* R.E.Fr.] have 'fruity' scents and cream or yellow petals, with Nitidulidae representing 94% or greater of the visitors observed (Table 1; Jürgens *et al.*, 2000). However, these species achieve their 'fruity' scents using different volatile compounds. This shows potential convergent evolution towards small beetle pollination, and illustrates the significance of floral scent characterization in an ecological and phylogenetic context. Although *Anaxagorea* A.St.-Hil., *Duguetia* A.St.-Hil., *Annona* L. and *Xylopia* L. utilize different biochemical building blocks, they all produce floral scents characteristic of food substrates or brood sites of Nitidulidae (Phelan & Lin, 1991; Nout & Bartelt, 1998; Peña *et al.*, 1999). Furthermore, the differences in compound class seen in the 'fruity' odours appear to group roughly by genus, suggesting that floral scent composition and the underlying biosynthetic pathways may have some phylogenetic utility in Annonaceae. The two *Anaxagorea* spp. have scents dominated by aliphatic compounds (primarily aliphatic esters). Both *Xylopia* spp. have floral scents dominated by aromatic compounds, primarily 2-phenylethyl alcohol (61.4%) in *X. aromatica* and methyl benzoate (38.6%) in *X. benthamii*. The floral scent of *D. asterotricha* is dominated by isoprenoid compounds and a number of unknown compounds not identified by class. The floral scent of *Annona neoinsignis* is dominated by naphthalene, although it was noted that naphthalene (the scent of moth-balls) might have been of anthropogenic origin (Jürgens *et al.*, 2000).

Floral scent composition in *Asimina* Adans. also demonstrates the potential utility of scent composition in evolutionary and ecological contexts. Floral scents of *Asimina* are qualitatively quite different from the 'fruity' scents described by Jürgens *et al.* (2000), with half the genus emitting 'yeasty' floral odours and the other half emitting 'sweet', 'pleasant' and 'waxy' scents (Table 1). Flowers with yeasty scents share a small size and maroon pigmentation and probably mimic food or brood sites of local pollinating insects (Goodrich & Raguso, 2009; K. Goodrich, unpubl. data). Alternatively, flowers with pleasant, sweet scents share white coloration and relatively larger floral dimensions, and probably represent a genuine advertisement of copious floral tissues, pollen and liquid exudates (Goodrich & Raguso, 2009; K. Goodrich, unpubl. data). On a finer

Table 1. Descriptions of floral scent, floral colour and pollinators for 93 species representing 30 genera of Annonaceae

Species (citation)	Location	Scent description	Floral colour†	Primary pollinator(s)
<i>Anaxagorea brevipes</i> Benth.* (7)	SA	Fruity, banana-like	Cream	Beetles
<i>Anaxagorea crassipetala</i> Hemsl. (2)	CA	Strong spicy, fruity; detectable from several metres	Creamy white	Flies and beetles
<i>Anaxagorea dolichocarpa</i> Sprague & Sandwith* (7)	SA	Fruity, banana-like, acetic	Light yellow	Beetles
<i>Anaxagorea manausensis</i> A.Timmerman (14)	SA	Fruity odours	Not reported	Beetles
<i>Anaxagorea phaeocarpa</i> Mart. (14)	SA	Fruity odours	Not reported	Beetles
<i>Anaxagorea prinoides</i> St.Hil. & A.DC.* (21)	SA	Strong, fruity, banana-like	Yellow	Beetles
<i>Annona ambotay</i> Aubl. (27)	SA	Fragrant	Dark red to yellowish red	Not reported
<i>Annona coriacea</i> Mart. (6)	SA	Somewhat unpleasant odour	Not reported	Beetles
<i>Annona cornifolia</i> A.St.-Hil. (6)	SA	Pleasant fruity odour	Yellow (purple)	Beetles
<i>Annona crassiflora</i> Mart. (6)	SA	Somewhat unpleasant odour	Not reported	Beetles
<i>Annona dioica</i> A.St.-Hil. (6)	SA	Somewhat unpleasant odour	Not reported	Beetles
<i>Annona glabra</i> Forssk.* (6, 18)	NA/SA	Heavy acetic scent; strongest at dusk	Cream (red)	Beetles
<i>Annona monticola</i> Mart. (6)	SA	Somewhat unpleasant odour	Not reported	Beetles
<i>Annona neoinsignis</i> H.Rainer (previously <i>Rollinia insignis</i> R.E.Fr.)* (7)	SA	Fruity, sweet	Yellow	Beetles
<i>Annona tomentosa</i> R.E.Fr. (6)	SA	Pleasant fruity odour	Not reported	Beetles
<i>Asimina incana</i> Exell* (4, 18, 8)	NA	Strong, pleasant, sweet, with slight acrid or waxy note as flowers enter male stage	White/cream (yellow)	Beetles
<i>Asimina longifolia</i> Kral* (4, 18, 8)	NA	Faint, sweet, slightly 'green', fragrant	White/cream (purple)	Beetles
<i>Asimina obovata</i> Nash* (12, 18, 8)	NA	Pleasant, sweet, not very strong	White/cream (purple)	Beetles
<i>Asimina reticulata</i> Shuttlew. ex Chapm.* (4, 18, 19, 8)	NA	Very sweet and pleasant	White/cream (purple)	Beetles (bees observed)
<i>Asimina pygmaea</i> Dunal* (12, 18, 8)	NA	Yeasty and cheesy; foetid	Maroon (maroon)	Beetles
<i>Asimina tetramera</i> Small* (18, 19, 8)	NA	Yeasty, weak, slight rootbeer note; foetid	Maroon (yellow)	Beetles
<i>Asimina parviflora</i> Dunal* (18, 20, 8)	NA	Yeasty, like baking bread, but slightly fruity; foetid	Maroon	Flies, beetles
<i>Asimina triloba</i> Dunal* (5, 15, 8)	NA	Yeasty, like red wine or baking bread; foetid	Maroon (yellow)	Flies, beetles

Table 1. Continued

Species (citation)	Location	Scent description	Floral colour†	Primary pollinator(s)
<i>Bocageopsis multiflora</i> (Mart.) R.E.Fr. (6, 14)	SA	Variable – somewhat sweet or rancid; slight rancid-fruity odour	Whitish	Thrips
<i>Bocageopsis pleiosperma</i> Maas (27)	SA	Sweet fragrance	Creamy yellow (pinkish)	Not reported
<i>Cananga odorata</i> (Lam.) Hook.f. & Thomson* (23)	SEA	Intensely sweet, similar to jasmine	Yellowish green to yellow	Not reported
<i>Cymbopetalum brasiliense</i> Benth.* (32)	SA	Balsamic; not fruit-like	Yellow	None observed
<i>Cymbopetalum torulosum</i> G.E.Schatz (25)	CA	Subtle odour reminiscent of linseed oil	Yellowish green to yellow	Beetles
<i>Deeringothamnus pulchellus</i> Small* (11, 18)	NA	Very sweet and perfume-like	White/cream	Possibly beetles or thrips
<i>Deeringothamnus rugelii</i> Small* (11, 18)	NA	Very faint, slightly rubbery or unpleasant	Yellow	Possibly flies or thrips
<i>Duguetia asterotricha</i> (Diels) R.E.Fr. (7)	SA	Fruity, pineapple-like	Yellowish	Beetles
<i>Duguetia cadaverica</i> Huber* (21)	SA	Mouldy, cheesy, foetid scent	Red (white)	Beetles
<i>Duguetia calycina</i> Benoist (26)	SA	Agreeable and intensifying at night (with thermogenesis)	Greenish-yellow to greenish-white	Beetles
<i>Duguetia flagellaris</i> Huber (26, 27)	SA	Odour similar to fruit juice of <i>Euterpe oleracea</i> (acai palm); sweet scent of overripe pineapples	Pink (red)	Beetles
<i>Duguetia furfuracea</i> (A.St.-Hil.) Saff. (26)	SA	Pleasant, fruity odour	Reddish	Beetles
<i>Duguetia lanceolata</i> A.St.-Hil. (14)	SA	Onset of anthesis – pleasant fruity odour; later anthesis – change to rotting fruit odour	Deep red petals	Beetles
<i>Duguetia marcgraviana</i> Mart. (30)	SA	Female stage is similar to mango or caja (<i>Spondias cytherea</i>); male stage is similar to formaldehyde mixed with fruit (strong and repugnant)	Brown to reddish	Beetles
<i>Duguetia neglecta</i> Sandwith (26)	SA	Initially agreeable ripe fruit odour, changing to unpleasant rotten fruit odour	Cream	Beetles
<i>Duguetia pycnastera</i> Sandwith (26)	SA	Smell of ripe peaches, changing to acetonetic fruit ester odour	Pale yellow	Beetles
<i>Duguetia riparia</i> Huber (26)	SA	Aromatic	Yellow	Beetles

Table 1. Continued

Species (citation)	Location	Scent description	Floral colour†	Primary pollinator(s)
<i>Duguetia stelechantha</i> (Diels) R.E. Fr. (26)	SA	Odour of ripe bananas, detectable from several metres	Yellow (wine-red)	Beetles
<i>Duguetia surinamensis</i> R.E.Fr. (27)	SA	Strong smell or a slightly sweet aroma	Cream, maturing dull red	Not reported
<i>Duguetia trunciflora</i> Maas & A.H.Gentry (27)	SA	Smell of bananas	Cream	Not reported
<i>Duguetia ulei</i> (Diels) R.E.Fr. (26, 27)	SA	Aromatic odour similar to squashed Myrtaceae leaves; mushroom-like odour	Cream-coloured	Beetles
<i>Encisanthum cf. paradoxum</i> Becc. (14)	SEA	Aromatic odour of ripe fruits	Yellowish-cream	Beetles, some flies
<i>Goniothalamus australis</i> Jessup (14)	AUST	Strong odour of fermented fruits	From green to yellow to deep brownish orange-red	Beetles
<i>Gutteria duodecima</i> Maas & Westra (31)	SA	Apple-like odour	Brownish-yellow	Not reported
<i>Gutteria foliosa</i> Benth. (14)	SA	Slight fruity scent, similar to ripe bananas	Yellow, becoming reddish-brown	Beetles
<i>Gutteria megalophylla</i> Diels (27)	SA	Aromatic	Pinkish-orange to red	Not reported
<i>Gutteria meliodora</i> R.E.Fr. (27)	SA	Aromatic	Green, maturing yellow	Not reported
<i>Gutteria neglecta</i> R.E.Fr. (6)	SA	Heavy, fruit-like odour	Yellowish, becoming brown	Beetles
<i>Gutteriopsis blepharophylla</i> (Mart.) R.E.Fr. (27)	SA	Pleasant smell	Whitish-yellow	Not reported
<i>Gutteriopsis hispida</i> R.E.Fr. (27)	SA	Pleasant smell	Yellow	Not reported
<i>Haplostichanthus</i> sp. F.Muell. (14)	AUST	Did not detect any floral odour	Pale green (white, wine-red)	Beetles
<i>Isolona campanulata</i> Engl. & Diels (28)	AF	Fruit-like, fermenting	Yellow (dark purple)	Beetles
<i>Meiogyne</i> sp. Miq. (14)	AUST	Strong emission similar to mushrooms during female and male phase	Pale yellow (red)	Beetles
<i>Meiogyne virgata</i> Miq. (14)	SEA	Female stage slightly fruity odour; male stage stronger, penetrating odour of rotten fruit	Yellowish	Beetles
<i>Melodorum fruticosum</i> Lour.* (29)	SEA	Strongly scented	Pale yellow	Not reported
<i>Melodorum</i> sp. Hook.f. & Thomson (14)	AUST	Sharp and acetone-like	Brown (cream)	Beetles
<i>Melodorum uhrii</i> F.Muell. (14)	AUST	Faint, aromatic, sweet, fruity, and apple-like note	Not reported	No visitors observed
<i>Monodora tenuifolia</i> Benth. (28)	AF	Sweetish, cabbage-like, similar to a rabbit hutch, mouldy, disagreeable	Yellowish with dark red spots	Flies, mostly dung flies
<i>Oxandra euneura</i> Diels (6)	SA	Sweet perfumed odour during female stage	Not reported	Beetles and thrips

Table 1. Continued

Species (citation)	Location	Scent description	Floral colour†	Primary pollinator(s)
<i>Piptostigma</i> sp. Oliv. (28)	AF	Fruity, apple-like	Light yellow	Beetles
<i>Polyalthia</i> cf. <i>cauliflora</i> Hook.f. & Thomson (14)	SEA	Very slight peach-like or resinous odour; later, slight peach – and yet stronger, straw-like odour	Carmin (cream white)	Did not detect floral visitors – self-pollination is likely
<i>Polyalthia coffeoides</i> (Thwaites) Hook.f. & Thomson (16)	SEA	Strong alcoholic to fermented fruit-like scent	Yellowish green	Beetles
<i>Polyalthia discolor</i> Diels (13)	SEA	Pleasing, strong, like <i>Cananga</i> <i>odorata</i>	Yellow	Beetles
<i>Polyalthia glauca</i> Boerl. (13)	SEA	Pleasing, strong, like <i>Cananga</i> <i>odorata</i>	Yellow	Beetles
<i>Polyalthia hypoleuca</i> Hook.f. & Thomson (13)	SEA	Pleasing, strong, like <i>Cananga</i> <i>odorata</i>	Yellow	Beetles
<i>Polyalthia korinti</i> (Dunal) Hook.f. & Thomson (16)	SEA	Strong alcoholic to fermented fruit-like scent	Vivid green	Beetles
<i>Polyalthia multinervis</i> Diels (13)	SEA	No odour detected	Yellow	Beetles
<i>Polyalthia sumatrana</i> King (13)	SEA	Pleasing, strong, like <i>Cananga</i> <i>odorata</i>	Yellow	Beetles
<i>Popowia pisocarpa</i> Endl. (9)	SEA	Strong odour throughout female and male phase; 'different' from other Annonaceae	Not reported	Thrips
<i>Pseuduvaria froggattii</i> (F.Muell.) Jessup (14)	AUST	Unpleasant scent reminiscent of old dishwater or vomit	Cream (wine-red, dark purple)	Flies and beetles
<i>Rollinia mucosa</i> Baill. (7)	SA	Fruity, sweet odour	Cream	Not reported
<i>Sapranthus isae</i> J.G.Vélez & Cogollo (24)	SA	Fragrant	Green (purple, black)	Not reported
<i>Sapranthus</i> sp. Seem. (14)	SA	Exhales an unpleasant odour	Dark purple or brown	Beetles, bees, possibly flies
<i>Sapranthus viridiflorus</i> G.E.Schatz (24)	SA	Lingering, strong foetid scent of carrion, similar to stapelias and aristolochias	Green (purple, white)	Not reported
<i>Tetrameranthus duckei</i> R.E.Fr. (6, 27)	SA	Musky odours (during the night); musky odour or strong fragrance of anise	Yellow	Beetles
<i>Unonopsis duckei</i> R.E.Fr. (27)	SA	Sweet scent	Cream	Not reported
<i>Unonopsis</i> <i>gutterioides</i> (A.DC.) R.E.Fr. (3, 27)	SA	Similar to lemongrass or vanilla, strongest in morning	Cream	Euglossine bees
<i>Unonopsis stipitata</i> Diels* (22)	SA	Strong, spearmint-like odour	Cream	Euglossine bees
<i>Uvaria elmeri</i> Merr. (10)	SEA	Odour like decayed wood or a mushroom, stronger during the male phase	Creamy white or brown	Cockroaches, flies

Table 1. *Continued*

Species (citation)	Location	Scent description	Floral colour†	Primary pollinator(s)
<i>Uvariodendron calophyllum</i> R.E.Fr. (28)	AF	Fruity, spicy, aromatic and sweet	Pale yellow (red)	Beetles
<i>Uvariodendron connivens</i> (Benth.) R.E.Fr. (28)	AF	Strong, aromatic and fruity	Greyish magenta	Beetles
<i>Uvariopsis bakeriana</i> (Hutch. & Dalziel) Robyns & Ghesq. (28)	AF	Faint, with sharp notes, pungent, spicy, nutmeg-like	Violet brown	Rare visitors, dung flies
<i>Uvariopsis congolana</i> (De Wild.) R.E.Fr. (28)	AF	Sharp, pungent, fungus-like, sulphur-like	Yellowish	Sporadic dung fly visitors
<i>Xylopiya amazonica</i> R.E.Fr. (27)	SA	Aromatic	Cream	Not reported
<i>Xylopiya aromatica</i> (Lam.) Mart.* (7)	SA	Sweet, aromatic	White	Thrips
<i>Xylopiya benthamii</i> R.E.Fr.* (7)	SA	Fruity, similar to ripe fruit of <i>Spondias lutea</i>	Yellowish	Beetles
<i>Xylopiya brasiliensis</i> Spreng. (1)	SA	Fruity odours	Pale colour	Beetles
<i>Xylopiya championii</i> Hook.f. & Thomson* (17)	SEA	Strong, fruity odour	Yellowish-cream	Beetles
<i>Xylopiya emarginata</i> var. <i>duckei</i> R.E.Fr. (27)	SA	Fruity odour	Yellow	Not reported
<i>Xylopiya spruceana</i> Benth. ex Spruce (27)	SA	Scented	Yellow (white)	Not reported

*Species with published chemical scent analyses.

†Floral colour listed is major/outer floral colour; inner colour is listed in parentheses, generally representing colour found on adaxial base of inner whorl petals, occasionally associated with patches of corrugate tissue, food bodies or glands.

Locality abbreviations: AF, Africa; AUST, Australia; NA, North America; SA, South America; SEA, South-East Asia.

1, Andrade *et al.* (1996); 2, Armstrong & Marsh (1997); 3, Carvalho & Webber (2000); 4, K. R. Goodrich, pers. obs.; 5, Goodrich *et al.* (2006); 6, Gottsberger (1999); 7, Jürgens *et al.* (2000); 8, Kral (1960); 9, Momose *et al.* (1998a); 10, Nagamitsu & Inoue (1997); 11, Norman (2003); 12, Norman & Clayton (1986); 13, Rogstad (1994); 14, Silberbauer-Gottsberger *et al.* (2003); 15, Willson & Schemske (1980); 16, Ratnayake *et al.* (2006); 17, Ratnayake *et al.* (2007); 18, Goodrich & Raguso (2009); 19, Cox (1998); 20, Norman *et al.* (1992); 21, Teichert (2008); 22, Teichert *et al.* (2008); 23, Ma *et al.* (1988); 24, Vélez-Arango & Cogollo-Pacheco (2007); 25, Schatz (1985); 26, Webber & Gottsberger (2003); 27, Maas *et al.* (2007); 28, Gottsberger *et al.* (2011); 29, Pripdeevech (2011); 30, Silva & Neta (2010); 31, Erkens *et al.* (2008); 32, Braun *et al.* (2011).

scale, the floral scent of yeasty maroon flowers shows potential diversification of mimicry types. Two species [*A. triloba* (L.) Dunal and *A. parviflora* (Michx.) Dunal] occur in mesic woodlands of temperate North America (Kral, 1960), and their scents are dominated by small aliphatic alcohols and esters associated with rotting fruits or fermenting sugars (Table 2; Goodrich

et al., 2006; Goodrich & Raguso, 2009). The other two species with yeasty scents contain many of the same aliphatic compounds, with the addition of dimethyl disulphide in *A. pygmaea* (W.Bartram) Dunal and indole in *A. tetramera* Small (Table 2; Goodrich & Raguso, 2009). Dimethyl disulphide and indole are characteristic of the scents of carrion and faeces,

Table 2. Floral scent chemical diversity by broad biosynthetic class for 24 species representing 11 genera of Annonaceae

Species (citation)	Location	Aliph hc	Aliph alc	Aliph eth	Aliph est & ket	Aliph ald & ket	Benz hc	Oxy benz	Mono hc	Oxy mono	Sesqui hc	Oxy sesqui	N-cmpds	S-cmpds
<i>Asimina triloba</i> (2)	NA	0	4 (0)	3 (0)	1 (0)	0	0	0	8 (0)	1 (0)	8 (0)	0	8 (4)	0
<i>Asimina parviflora</i> (3)	NA	0	3 (0)	9 (2)	3 (2)	0	1 (1)	0	3 (0)	0	17 (0)	0	0	0
<i>Asimina tetramera</i> (3)	NA	1 (0)	4 (0)	1 (0)	1 (0)	0	2 (0)	0	7 (0)	1 (0)	8 (0)	0	2 (0)	0
<i>Asimina pygmaea</i> (3)	NA	3 (0)	3 (0)	1 (0)	2 (0)	0	0	0	5 (0)	1 (0)	14 (0)	0	1 (0)	1 (1)
<i>Asimina obovata</i> (3)	NA	3 (0)	0	1 (0)	1 (0)	0	1 (1)	0	7 (0)	9 (1)	12 (0)	1 (0)	0	0
<i>Asimina incana</i> (3)	NA	5 (1)	0	1 (0)	3 (0)	0	0	0	7 (0)	12 (2)	13 (0)	1 (0)	1 (0)	0
<i>Asimina reticulata</i> (3)	NA	4 (1)	0	0	1 (0)	0	4 (0)	0	5 (0)	3 (0)	11 (0)	0	1 (0)	0
<i>Asimina longifolia</i> (3)	NA	4 (1)	2 (1)	1 (0)	1 (0)	0	0	0	3 (0)	6 (0)	9 (0)	0	1 (0)	0
<i>Deeringothamnus rugelii</i> (3)	NA	1 (0)	0	1 (0)	2 (1)	0	1 (0)	0	4 (0)	3 (1)	6 (0)	1 (0)	2 (0)	0
<i>Deeringothamnus pulchellus</i> (3)	NA	0	0	3 (1)	0	0	6 (1)	0	2 (0)	3 (0)	6 (0)	1 (0)	3 (0)	0
<i>Annona glabra</i> (3)	NA/SA	0	3 (2)	1 (0)	1 (1)	0	0	0	9 (0)	2 (0)	2 (0)	0	0	0
<i>Anaxagorea brevipes</i> (4)	SA	1 (0)	0	8 (7)	0	0	0	0	4 (0)	1 (0)	4 (0)	0	0	0
<i>Anaxagorea dolichocarpa</i> (4)	SA	1 (0)	0	11 (4)	1 (0)	3 (0)	2 (0)	0	3 (0)	0	3 (0)	0	1 (1)	0
<i>Anaxagorea prinoides</i> (8)	SA	0	1 (0)	6 (2)	0	0	0	0	0	0	0	0	0	0
<i>Annona neoinsignis</i> (previously <i>Rollinia insignis</i>) (4)	SA	1 (0)	0	0	1 (0)	6 (0)	1 (0)	0	3 (0)	0	9 (0)	0	0	0
<i>Unonopsis stipitata</i> (9)	SA	0	0	0	0	0	0	0	12 (2)	8 (6)	0	0	0	0
<i>Cymbopetalum brasiliense</i> (1)	SA	0	0	0	0	0	2 (1)	0	0	0	0	0	0	0
<i>Duguetia asterotricha</i> (4)	SA	2 (1)	0	0	0	1 (0)	0	0	3 (0)	0	6 (0)	0	0	0
<i>Duguetia cadaverica</i> (8)	SA	0	4 (4)	1 (1)	0	0	0	0	0	0	0	0	0	2 (2)
<i>Xylopia aromatica</i> (4)	SA	1 (0)	0	0	1 (0)	3 (0)	6 (1)	0	6 (0)	2 (2)	9 (0)	0	1 (0)	0
<i>Xylopia benthamii</i> (4)	SA	1 (0)	0	0	0	6 (0)	2 (0)	0	3 (0)	1 (0)	5 (0)	0	0	0
<i>Xylopia championii</i> (7)	SEA	0	0	8 (7)	0	0	0	0	5 (3)	4 (3)	7 (4)	1 (1)	0	0
<i>Cananga odorata</i> (5)	SEA	0	0	4 (3)	0	0	3 (1)	0	0	1 (0)	0	0	0	0
<i>Melodorum fruticosum</i> (6)	SEA	0	0	5 (3)	0	0	5 (3)	0	14 (4)	6 (5)	20 (10)	4 (4)	0	0

Values reported as number of different compounds within each compound class, with compounds unique to each species in parentheses. Locality abbreviations: NA, North America; SA, South America; SEA, South-East Asia. Chemical class abbreviations: Aliph hc, aliphatic hydrocarbons; Aliph alc, aliphatic alcohols; Aliph est & eth, aliphatic esters and ethers; Aliph ald & ket, aliphatic aldehydes and ketones; Benz hc, benzenoid hydrocarbons; Oxy benz, oxygenated benzenoids; Mono hc, monoterpene hydrocarbons; Oxy mono, oxygenated monoterpenoids; Sesqui hc, sesquiterpene hydrocarbons; Oxy sesqui, oxygenated sesquiterpenoids; N-cmpds, nitrogen-containing compounds; S-cmpds, sulphur-containing compounds.

1, Braun *et al.* (2011); 2, Goodrich *et al.* (2006); 3, Goodrich & Raguso (2009); 4, Jürgens *et al.* (2000); 5, Ma *et al.* (1988); 6, Pripdeevech (2011); 7, Ratnayake *et al.* (2007); 8, Teichert (2008); 9, Teichert *et al.* (2008).

respectively. Both *A. pygmaea* and *A. tetramera* occur in dry, sandy pine scrub habitats in Florida, USA (Kral, 1960), and the addition of dimethyl disulphide or indole may represent a transition towards mimicry of food sources more common to these habitats. This diversification of mimicry types has been demonstrated previously in Araceae and several stapeliads (Apocynaceae; Stensmyr *et al.*, 2002; Jürgens *et al.*, 2006). Evolutionarily, the two broad scent types of *Asimina* may represent a single divergence or multiple transitions between suites of floral traits. In addition, the visual displays of white-flowered *Asimina* spp. are strikingly similar, whereas the species-specific scent blends are quite distinct. It will be interesting to examine the role of floral scent in reproductive isolation of sympatric taxa, potentially through odour-mediated floral constancy (see Wright & Schiestl, 2009).

The remaining scent studies of Annonaceae are of more isolated taxa and generally illustrate the role of scent in highly specialized pollination systems (Ma *et al.*, 1988; Ratnayake *et al.*, 2007; Teichert, 2008; Teichert *et al.*, 2008, 2011; Braun *et al.*, 2011; Pripdeevech, 2011). Four other New World species of Annonaceae were studied [*Duguetia cadaverica* Huber, *Anaxagorea prinoides* (Dunal) A.DC., *Unonopsis stipitata* and *Cymbopetalum brasiliense* (Vell.) Benth. ex Baill.; Teichert, 2008; Teichert *et al.*, 2008, 2011; Braun *et al.*, 2011], with scent playing a central role in at least three distinctly different and specialized pollination syndromes. *Anaxagorea prinoides* has a relatively simple scent blend (only seven compounds) described as strong and banana-like (Teichert *et al.*, 2011). The pollination strategy of this species appears to conform to the small beetle pollination observed for *Anaxagorea dolichocarpa* and several other species, described by Jürgens *et al.* (2000). *Unonopsis stipitata* emits high levels of several monoterpenes, including limonene and carvone and their oxides, found to be highly attractive to male euglossine bees (Teichert *et al.*, 2008), and these bees have been documented as the main floral visitors. One other species of Annonaceae, *Unonopsis gatteroides* (A.DC.) R.E.Fr., has been shown to be pollinated by male euglossine bees (Carvalho & Webber, 2000). No floral scent analyses have been performed on this species, but the scent has been described as similar to lemon grass or vanilla (Table 1; Carvalho & Webber, 2000).

The floral scent of *D. cadaverica* is described as 'mouldy', 'cheesy' and 'mushroom-like', with (*E*)-2-octen-1-ol and (*Z*)-1-octen-5-ol as the main compounds (Table 1; Teichert, 2008). These eight-carbon alcohols are typical of mushroom odour (Picardi & Issenberg, 1973) and, with the fleshy red and white petals and occurrence of flowers along flagelliform twigs at

ground level, yield convincing mushroom mimics. This mimicry observation is supported by the attraction of mycetophagous beetles as pollinators (Teichert, 2008). An odour similar to mushrooms has also been described for two Asian species (*Uvaria elmeri* Merr. and an unidentified species of *Meiogyne* Miq.; Nagamitsu & Inoue, 1997 and Silberbauer-Gottsberger *et al.*, 2003, respectively), the African species *Uvaropsis congolana* (De Wild.) R.E.Fr. (Gottsberger *et al.*, 2011) and the South American species *Duguetia ulei* (Diels) R.E.Fr. (Maas, Maas & Miralha, 2007), suggesting that this type of mimicry has evolved at least several times in the family. It will be interesting to see whether eight-carbon alcohols or ketones dominate the floral scent of these other species characterized as having 'mushroom' or 'fungus-like' odours.

Finally, flowers of *Cymbopetalum brasiliense* emit a 'balsamic' scent which is 'not reminiscent of fruit' (Braun *et al.*, 2011). The scent of *C. brasiliense* is uncharacteristically simple for Annonaceae, consisting mostly of *p*-methyl anisol (> 99% relative scent composition), with small quantities of *p*-cresol (Braun *et al.*, 2011). Braun *et al.* (2011) observed few floral visitors and agamospermic fruit production in *C. brasiliense*, providing the first documented case of probable apomixis in Annonaceae. *p*-Methyl anisol, however, is also a key floral scent component (> 99% relative scent composition) for several species of *Phytelephas* Ruiz & Pav. (Ervik, Tollsten & Knudsen, 1999) and, in field bioassays, Ervik *et al.* (1999) found that numerous insects were attracted to filter paper soaked in *p*-methyl anisol. These contradictory results may reflect variation in pollinator communities, or a product of the forest fragmentation surrounding populations of *C. brasiliense* documented by Braun *et al.* (2011).

Only three Old World species of Annonaceae have had their floral scent composition analysed: *Xylopia championii* Hook.f. & Thomson (Ratnayake *et al.*, 2007), *Cananga odorata* (Lam.) Hook.f. & Thomson (Ma *et al.*, 1988) and *Melodorum fruticosum* Lour. (Pripdeevech, 2011). Ratnayake *et al.* (2007) described the scent of *X. championii* as strong and fruity, dominated by caproic acid, an ethyl ester of hexanoate and ethyl decadienoate. In this case, floral odour emission is strongly correlated with floral reproductive phase and floral thermogenesis. These traits, in combination with small floral dimensions, indicate that this species is specialized for its observed curculionid beetle pollinators (Ratnayake *et al.*, 2007). The studies of *Cananga odorata* (Lam.) Hook.f. & Thomson and *Melodorum fruticosum* Lour. do not present the data in the context of pollination strategies. *Cananga odorata* (commonly known as ylang-ylang) is highly valued for its floral essential oils (Manner & Elevitch, 2006) which yield a heavy, sweet

scent, but little is known about its reproductive biology. Ma *et al.* (1988) reported the floral volatiles of *Cananga odorata* to include ethyl, propyl, butyl and pentyl acetates, several benzenoid compounds and linalool (a monoterpene alcohol). A number of studies have documented bioactive constituents from bark, leaves, branches and flowers of *M. fruticosum* (Jung *et al.*, 1990; Tuchinda *et al.*, 1991; Pripdeevech & Chukeatirote, 2010), but little work has been carried out on its pollination biology. Pripdeevech (2011) characterized the floral scent for *M. fruticosum* using three types of SPME fibres to illustrate the variation that this technique may potentially yield (as discussed earlier in this article). Although the relative percentages of floral compounds varied by fibre type, all fibre types showed the floral scent of *M. fruticosum* to contain relatively large quantities of *p*-methyl anisol (a benzenoid compound discussed for *C. brasiliense*, above) and the monoterpenes β -phellandrene, *trans*- β -ocimene and linalool, with each of these compounds representing >5% relative scent composition for most or all of the sampling techniques used (Pripdeevech, 2011).

FLORAL SCENT CHEMICAL DIVERSITY IN ANNONACEAE

A summary of the diversity of floral scent composition for all sampled species of Annonaceae is provided in Table 2. Several conclusions can be drawn from the diversity of floral scent composition in species of Annonaceae studied to date. First, it is interesting to compare scent composition and diversity between genera, although this comparison is limited by the number of species sampled within each genus. For example, the three *Anaxagorea* spp. sampled show relatively high diversity in aliphatic esters compared with the other genera, and these compounds are probably responsible for the strong 'fruity' aromas characteristic of these species. *Asimina* shows relatively high frequency and diversity of aliphatic hydrocarbons, aldehydes and ketones compared with all other genera sampled. Finally, oxygenated benzenoid compounds occur with almost complete absence of benzenoid hydrocarbons in *Asimina* and *Deeringothamnus* Small, whereas they are frequently associated with benzenoid hydrocarbons in *Anaxagorea*, *Annona* and *Xylopia* spp.

This comparison of floral scent diversity and composition may also be indicative of shared ecology and/or pollination strategy. For example, relatively high proportions of aliphatic alcohols are found in maroon-flowered *Asimina* spp. and *D. cadaverica* and, in combination with the red or maroon pigmentation of these species, may be linked to specialized food

mimicry pollination strategies (Teichert, 2008; Goodrich & Raguso, 2009). Furthermore, the dimethyl oligosulphides, found only in *A. pygmaea* and *D. cadaverica* (Teichert, 2008; Goodrich & Raguso, 2009), may represent specialization towards specific mimicry of protein decomposition typical of carrion or faeces. The eight-carbon alcohols of *D. cadaverica* are highly indicative of mushroom mimicry (see discussion above), but the oligosulphides may mimic substrates on which mushrooms may occur. Finally, the relatively high number of aliphatic hydrocarbons found in six *Asimina* spp. may be linked to adaptations preventing desiccation (see Hadley, 1981), as these species occur in xeric pine scrub habitats (Kral, 1960), unlike most other sampled *Asimina* spp. from mesic tropical or temperate forests.

The absence of certain compound classes may also be evolutionarily or ecologically informative. For example, sesquiterpene hydrocarbons appear to be relatively diverse and ubiquitous (high numbers and low 'unique' representation in Table 2) in the floral scent of many species, and it is therefore interesting that this class of compounds is not reported for four species. This result, however, may be an artefact of the differing interpretations of floral scent data by individual researchers. Sesquiterpenes are frequently associated with leaf odours in Annonaceae (Oguntimein *et al.*, 1989; Fekam Boyom *et al.*, 1996; Maia *et al.*, 2005; K. Goodrich, unpubl. data). Their absence in floral scent analyses by Ma *et al.* (1988), Teichert (2008), Teichert *et al.* (2008) and Braun *et al.* (2011) may reflect the absence of these compounds from floral scent altogether, their absence in concentrations or proportions above those of vegetative odours, or the authors' decision to report only compounds unique to floral tissue. Perhaps more informative is the almost complete absence of oxygenated monoterpenes from sampled species of *Anaxagorea* and *Duguetia*, and the absence of both oxygenated and hydrocarbon benzenoid compounds from Old World *Xylopia championii*, compared with their relative abundance in the two New World *Xylopia* spp. There is also a notable lack of nitrogenous compounds in tropical species sampled compared with the temperate species of *Asimina* and *Deeringothamnus*. However, given the nested phylogenetic position of *Deeringothamnus* in *Asimina* (R. Abbott, Department of Biological Sciences, Eastern Illinois University, Charleston & K. Neubig, Department of Biology, University of Florida, Gainesville, pers. comm.), the presence of nitrogenous compounds in this clade is a result of shared ancestry. Whether this is a result of differences between temperate and tropical habitats is difficult to test as the *Asimina*–*Deeringothamnus* clade is the only temperate group in Annonaceae, and therefore no further comparisons of tropical and temperate sister groups can be made.

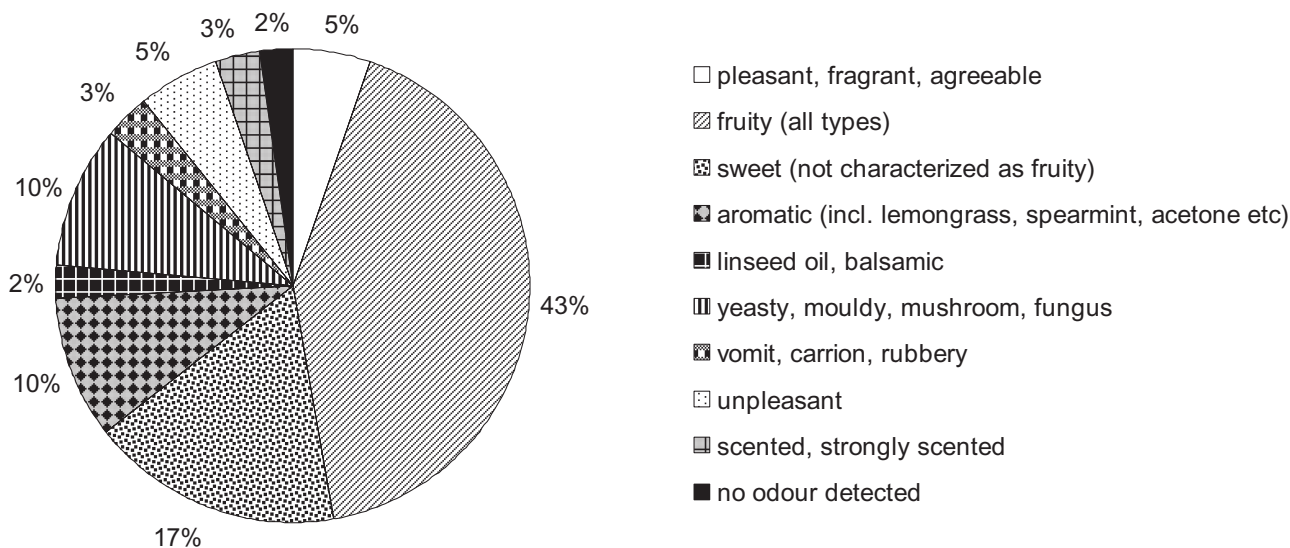


Figure 1. Annonaceae scent 'types' based on descriptions of 93 species.

As a final point, it is interesting and informative to compare the similarities and differences between entire scent datasets. Jürgens (2009) illustrated the potentially strong link between overall floral scent composition and pollination strategy by conducting a multivariate analysis of 150 identified compounds across 21 species of Annonaceae. Jürgens (2009) then demonstrated how species which group by similarity of scent composition also group roughly by pollination strategy. This type of meta-analysis becomes increasingly informative as scent studies are performed across additional species and genera.

PERCEPTUAL DESCRIPTIONS OF FLORAL SCENT IN ANNONACEAE

Several scent 'types' are clearly recognizable in Annonaceae, including several variations of 'fruity', 'aromatic', 'sweet (but not fruit-like)' and 'mushroom-like', even without extensive chemical analyses. Scent descriptions from the literature have been compiled in Table 1. I then subjectively categorized the scent descriptions (based on the descriptions provided for 93 species) to provide a more general overview of the frequency of scent types currently described in the family (Fig. 1). Although these perceptual depictions are subjective and may vary somewhat by author, these depictions of floral scent give some clues to the possible chemical composition of the scent. One of the most common scent descriptions mentioned in the existing literature for the family is 'fruity' (Fig. 1), which is often further qualified as 'fruity and sweet', 'ripe fruit' or 'rancid/rotting fruit'. Typical fruit odours are usually associated with ripe fruits, close to or at an early stage of decay. Although the smell of ripe

fruit from different families and genera varies, common ripe fruit odours consist of a blend of branched aliphatic esters, alcohols and lactones (Macku & Jennings, 1987; Horvat *et al.*, 1990; Shiota, 1991; Augusto *et al.*, 2000; Carasek & Pawliszyn, 2006). As a fruit becomes more rotten, its scent noticeably becomes more fermented or alcoholic (a sharper, unpleasant odour). Several protogynous species of Annonaceae [*Meiogyne virgata* (Blume) Miq., *Duguetia lanceolata* A.St.-Hil., *D. marcgraviana* Mart., *D. neglecta* Sandwith and *D. pycnastera* Sandwith] are described as having pleasant or slight 'fruity' odours during their female phase, which change to more 'rotten' or 'rancid' fruit odours as they progress through the male stage (Silberbauer-Gottsberger *et al.*, 2003; Webber & Gottsberger, 2003; Silva & Neta, 2010). Studies of fermentation volatiles typically show the presence of ethanol, ethyl acetate, 3-methyl-1-butanol and 3-hydroxy-2-butanone (Lee *et al.*, 1997; Goodrich *et al.*, 2006; Gürbüz, Rouseff & Rouseff, 2006), and these compounds may potentially be found in floral odours mimicking rotten fruits, as they are also seen in the 'yeasty' odour of some *Asimina* spp. (Goodrich & Raguso, 2009).

The most common specific 'fruity' odour in Annonaceae is 'banana-like', often found in combination with descriptions of an 'alcoholic' or 'acetic' scent (Table 1). The odour of ripe bananas was described for *Anaxagorea dolichocarpa*, *A. brevipes*, *A. prinoides*, *Duguetia stelechantha* (Diels) R.E.Fr., *D. trunciflora* Maas & Gentry and *Guatteria foliosa* Benth. (Jürgens *et al.*, 2000; Silberbauer-Gottsberger *et al.*, 2003; Webber & Gottsberger, 2003; Maas *et al.*, 2007). Existing data on the odour composition of ripe bananas show it to be dominated by esters of acetic,

butanoic and 3-methylbutanoic acid, alcohols and one ketone (Macku & Jennings, 1987). Chemical odour analysis for the above *Anaxagorea* spp. shows that their scents are, in fact, dominated by the same or similar esters (Jürgens *et al.*, 2000; Teichert, 2008). Floral scent analyses for *Guatteria foliosa*, *Duguetia stelechantha* and *D. trunciflora* have not yet been published.

Other descriptions of 'fruity' Annonaceae floral scents include comparisons to ripe cajá (*Spondias lutea* L.), pineapple [*Ananas comosus* (L.) Merr.], peaches [*Prunus persica* (L.) Stokes] and apples (*Malus domestica* Borkh.). Jürgens *et al.* (2000) compared the scent of *X. benthamii* flowers to the scent of ripe fruit of *S. lutea* (Anacardiaceae). The chemical analysis of *X. benthamii* shows the scent to be dominated by methyl benzoate (38.6%), a heavy, sweet scent (Jürgens *et al.*, 2000). A chemical analysis of the scent of ripe *S. lutea* fruit has shown that its scent also contains methyl benzoate, with a number of other esters, alcohols and terpenoid compounds (Augusto *et al.*, 2000). *Duguetia asterotricha* and *D. flagellaris* Huber both have odours described as similar to ripe pineapple (Jürgens *et al.*, 2000; Webber & Gottsberger, 2003). The floral scent composition of *D. asterotricha* has a relatively high concentration of terpenoid compounds, including the monoterpenes limonene, *p*-cymene and α -pinene, but lacks oxygenated aliphatic compounds which are prevalent in the odour of fresh pineapple (Tokitomo *et al.*, 2005). In this case, human perception may not indicate chemical similarities between the floral scents of *D. asterotricha* and pineapple. However, there are a number of unidentified compounds in the floral scent of *D. asterotricha* (28% of the relative scent composition; Jürgens *et al.*, 2000), and thus a comprehensive comparison of the two scent blends is not possible.

Polyalthia cf. cauliflora Hook.f. & Thomson and *Duguetia pycnastera* are both described as having peach-like odours, whereas *Uvaria uhrii* (F.Muell.) L.L.Zhou, Y.C.F.Su & R.M.K.Saunders, *Guatteria duodecima* Maas & Westra and an unidentified *Piptostigma* spp. are all described as having an 'apple-like' odour (Silberbauer-Gottsberger *et al.*, 2003; Erkens, Westra & Maas, 2008; Gottsberger *et al.*, 2011). The scent of ripe peaches is dominated by lactones (Horvat *et al.*, 1990), and the scent of a ripe apple is dominated by α -farnesene (Matich, Rowan & Banks, 1996). It will be interesting to determine whether or not these compounds are major (or minor) components of the floral scent for these species.

CONCLUSIONS

Many of the points discussed above can only be supported with additional extensive testing, especially of

species closely related to those already sampled. Currently, most genera of Annonaceae lack published descriptions of floral scent. Of the genera with some scent characterization, most have scent descriptions (chemical or perceptual) for fewer than four species. In addition, I have found no studies documenting floral scent variation within or between populations of Annonaceae. Only two genera (*Asimina* and *Deeringothamnus*) have had their floral scent analysed for all species (Goodrich & Raguso, 2009), and these genera demonstrate the potential utility of floral scent in closely related taxa when assessing shared phylogenetic history versus (or in combination with) shared ecological contexts, including pollination strategies. Future work may also focus on evolutionarily divergent taxa in shared ecological contexts. For example, the convergence of fruity, sweet scents and light floral coloration associated with beetle pollination in a common habitat type (tropical rainforest near the Manaus region of Brazil) demonstrates the ecologically informative potential of floral scent analysis (Jürgens *et al.*, 2000). In this case, the varied composition, but similar quality, of floral scent represents the potential for convergent evolution of the same pollination syndrome in Annonaceae in evolutionarily divergent genera (Jürgens *et al.*, 2000).

In conclusion, floral scent in Annonaceae can be highly dynamic, with variation between floral organs or ontogenetic stage (as described by Goodrich & Raguso, 2009 and Ratnayake *et al.*, 2007, respectively), indicating the necessity for detailed spatial and temporal floral scent analyses within individual species and broad surveys across closely related species and genera. Advances in sampling and analytical techniques described earlier in this article have made it possible for such comprehensive studies. As more studies link distinctive floral scents to specialized pollination strategies in Annonaceae, it will become increasingly important to have detailed analyses of these scents; it will also become important to consider floral scent in contexts beyond pollinator attraction, including its potential role in herbivore and microbial inhibition, crypsis, pleiotropy and shared ancestry. The growing literature of floral scent analyses should lead to a better shared vocabulary of floral scent. At the very least, authors may note the presence or absence of floral scent as a potentially important component of floral display. Beyond presence/absence, it is becoming more common for authors to note qualities of floral odour, from simple descriptions of either 'pleasant' or 'unpleasant', to more detailed comparisons with commonly known scents, such as 'bananas', 'pineapple', 'mushrooms' or 'carrion'. Subjective descriptions, although potentially variable and imprecise, offer extremely valuable

information about overall floral display and the potential for future scent analyses. The knowledge to be gained from floral scent analyses in Annonaceae is phenomenal. All that remains is the time and enthusiasm to pursue such studies.

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