An understanding of the biochemical foundation for plant-pollinator interactions

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Abstract
Pollination is an ecosystem service performed by many of entities, majorly are animals like insects, birds, bats etc. This is mutually beneficial for both the organisms where some get their foods as rewards, while others benefited by reproduction. The majority of pollinators that routinely visit flowers to acquire nectar, pollen, and other things accidentally pollinate them, which leads to fruit set and reproduction of blooming plants. In their environment, plants emit a variety of chemical cues that have an impact on how animals interact with them while visiting. For example, pollinators' attractiveness to plant sources is influenced by factors like flower colour, floral perfume, pollen quality, and nectar nutritional value. This review article explores the chemical perspective of mutualism between plants and pollinators.

Keywords: Pollination, chemical cues, flower colour, floral perfume, pollen quality, nectar nutritional value, plant-pollinator mutualism

Introduction
The maintenance of the world's biodiversity and the security of our food supply depend on interactions between pollinators and the plants that serve as their hosts. The biodiversity of this planet depends on partnerships between plants and their pollinators, with an estimated 87.5% of all blooming plants relying to some extent on animal pollination (Ollerton et al., 2011) [34]. These connections frequently benefit both parties. While pollinators are rewarded by plants through the availability of food resources and/or a secure location to shelter, mate, oviposit, and develop, plants profit from animals through the movement of pollen between plants, ensuring fertilisation and gene flow.

The tremendous diversity of their blooms with regard to form and features like colour, scent, and nectar is a noteworthy characteristic of angiosperms that need animals as pollen conveyors to sexually reproduce. These characteristics are supported by the creation of secondary metabolites that plants utilise to entice and reward animal pollinators, such as pigments and volatiles in addition to carbohydrates and amino acids. Almost every group of plants has a unique strategy for luring pollinators, and there are a staggering number of morphological modifications to the various animal pollinators that are available to plants. These factors, along with the fact that pollination biology is such a vast topic, contribute to how complex and appropriate this relationship between plant and animal is. Additionally, there is the phenomenon of flower constancy, which has had a significant impact on how angiosperms and their animal partners have evolved together. It symbolises the dedication of a pollinator to consistently visit just a small number of plant species, and in some cases, just one. Floral morphology, aroma, and petal colour all influence this fidelity. In fact, many plants have purposefully limited themselves to pollination by a single type of vector through the evolution of their floral parts, giving rise to the so-called "bee flowers" (with short, wide corollas), "butterfly flowers" (with medium-length, narrow corollas), or "humming bird flowers" (with long, narrow corollas). For their part, animals grow specialised and reliant on a limited number of species, and finally just one plant, within the range of plants they can pollinate. This can be due to a distinctive blossom scent, a wealth of nectar, or some other attraction. Both plants and animals can greatly benefit from this mutual co-evolution.
Almost every species of the fig genus, *Ficus*, has its own species of chalcid wasp to pollinate it, illustrating it in severe forms. Similar examples can be seen in the Orchidaceae family, where specific species of *Ophrys* are pollinated only by an Andrena bee. Despite the fact that pollination ecology has been extensively written about (Faegri and van der Pijl, 1979; Kevan and Baker, 1983; Real, 1983) [14, 28], biochemical aspects have only sometimes been thoroughly examined. The current account is an effort to compile the majority of the data on this ecological subject that is currently available.

The role of flower signals in plant-pollinator communication
Plants that rely on biotic pollination to reproduce sexually alert animal pollen vectors to the existence of floral rewards by their scent and colour, and they subsequently reward these visits with nectar and pollen. Plants used colour, odour, and nectar and pollen composition in this chemical and visual interaction with their pollinators, as the phenotypic expression of the metabolic resources. New mechanisms for the production of floral metabolites have been discovered recently, and new theories have been developed about the buildup of pigments and release of aroma. Concurrently, research in the area of plant-insect communication has uncovered the role played by specific floral signals in luring pollinators.

Generally speaking, floral signals can be ‘honest signals,’ indicating the presence or quantity of reward in a bloom. Direct honest signals emanate directly from the reward, such as the scent of nectar and pollen, or humidity (Rahuso, 2004; Von Arx *et al*., 2012) [37, 48]. Alternatively, although emanating from different sections of the flower, floral signals may have a quantitative association with reward (Knauer and Schiestl, 2015) [29]. The size of the bloom is a common illustration, as larger flowers may yield more rewards. A particular volatile may occasionally be linked to reward, such as phenylacetaldehyde in *Brassica rapa* (Knauer and Schiestl, 2015) [29]. Phenylacetaldehyde and nectar production have no known physiological relationship, hence this correlation has most likely developed as a result of pollinators’ selection. In fact, pollinators might choose plants that give honest signals since it makes them more effective hunters, and they might punish ‘cheaters’ by avoiding them after a visit.

Clearly, not all flowery messages are sincere, which adds a compelling aspect to the scenario. As an illustration, many plants with spectacular blossoms never yield any benefits (Schiestl and Johnson, 2013) [41]. Although it has separately developed in many other plant groups, such compulsory rewardlessness is particularly prevalent in orchids (Renner, 2006) [40]. Floral mimicry, in which the flowers copy a “model” such as an oviposition substrate or a mating partner, is occasionally the outcome of this process.

Although there are still many unknowns regarding the biochemistry of floral mimicry, mimicry offers some fascinating examples of convergent biochemical evolution, such as desaturase enzymes in plants whose by-products imitate insect sex pheromones.

Colour of Flowers
The first and most well-known researchers to bring out several instances of floral features that have coevolved with the physical and physiological traits of their respective pollinators were Sprengel and Darwin (Dafni *et al*., 1997; Chittka *et al*., 2001; Waser and Ollerton, 2006) [10, 9, 49]. The floral coloration, which developed as an advertisement for pollinators, is one of the most remarkable characteristics.

Colour Preferences of Pollinators
The work of von Frisch (1950) [50] and others has greatly contributed to the wealth of knowledge that exists concerning bees’ preferred colours. They are known to favour colours that appear to humans to be blue and yellow. They are sensitive to the highly UV-absorbing flavones and flavonols, which are present as such in almost all white flowers and also occur as co-pigments in cyanic flowers, and they can also distinguish variances in absorption in the UV portion of the spectrum.

Even if pollinators have an innate preference for specific colours, there are two reasons why real flower selection in natural communities might not correspond to these preferences. First, in a natural setting, the number and presence of other co-pollinators may have an impact on the flower selection by potentially competing for flower resources (Lazaro *et al*., 2009) [36]. Second, pollinators may employ certain colours as signals for floral rewards, which could allow associative learning to modify initial inherent preferences (Gumbert, 2000; Goyret *et al*., 2008) [18, 17]. Individual pollinators are known to be remarkably flexible and will change plants in response to variations in pollen or nectar concentrations (Heinrich, 1979) [22]. As a result, the relationship between innate and learned preferences will determine how much colour influences final flower selection.

Other pollinators’ colour preferences have received less attention, however the information that is currently accessible is compiled in Table 1 with some figures.

<table>
<thead>
<tr>
<th>Animal</th>
<th>Flower colour preferences</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bees</td>
<td>Yellow and blue intense colours, also white</td>
<td>Can see in UV, but not sensitive to red</td>
</tr>
<tr>
<td>Butterflies</td>
<td>Vivid colours, including reds and purples</td>
<td>Mostly pollinate at night</td>
</tr>
<tr>
<td>Moths</td>
<td>Reds and purples, white or pale pinks</td>
<td></td>
</tr>
<tr>
<td>Wasps</td>
<td>Browns</td>
<td></td>
</tr>
<tr>
<td>Beetles</td>
<td>Dull, cream or greenish</td>
<td>Poor colour sense</td>
</tr>
<tr>
<td>Flies</td>
<td>Dull, brown, purple or green</td>
<td>Chequered pattern may be present</td>
</tr>
<tr>
<td>Birds</td>
<td>Vivid scarlets, also bicolours (red-yellow)</td>
<td>Sensitive to red</td>
</tr>
<tr>
<td>Bats</td>
<td>White or drab colours, e.g. greens and pale purples</td>
<td>Mostly colour-blind</td>
</tr>
</tbody>
</table>

Source: Abrol, 2012 [1]
Chemical Underpinnings of Flower Colour

The presence of pigments in chromoplasts or cell vacuoles of floral tissues is largely responsible for the colour of flowers. Plants lack the colours that are formed by the reflection and refraction of light from cell surfaces, which are so significant in the animal kingdom. The flavonoids are the most significant category of flower pigments since they provide cyanic colours (orange, red, and blue), as well as yellow and white (Harborne, 1988) [19]. The carotenoids are the only other significant category, and they mostly produce yellow shades with some orange and red. The classes of chlorophylls (greens), quinones (occasional reds and yellows), and betalain alkaloids (yellow, red, and purple colours in Centrospermae) are significantly less significant in terms of floral colouring.

The Change in Flower Colour

At the species level, evolutionary variations in flower colour can also be seen. Within a generation or two, plants may need to change the colour of their flowers to accommodate shifting pollinator populations. The red gilia, *Ipomopsis aggregata* is a good example of how plants can adapt quickly to shifting pollinators. It has been noted that in populations near Flagstaff, Arizona, a small proportion of plants undergo a seasonal blossom colour change from red to pinkish-white (Paige and Whitham, 1985) [35]. The change is perfectly associated with the mid-July southern emigration of hummingbirds, which are the principal pollinators, and the requirement to attract another pollinator, a hawkmoth called *Hyies lincata*. The amount of anthocyanin produced in the petal is diluted during colour shifting, which can take place within the same inflorescence, and eventually anthocyanin synthesis is completely stopped. Variation in plant colour *Ipomopsis* offers a system to guarantee that the pollinators active at a specific moment are most successfully drawn to the bloom. After pollination, flowers may undergo colour changes, such as going from yellow (carotenoid) to red (anthocyanin), as shown in *Lantana camara* (Fig. 5). This is brought on by the pollinator removing nectar from the nectary (Eisikowitch and Lazar 1987) [13], and such colour shifts is beneficial for both sides. They increase the effectiveness of pollination and nectar collection by directing the pollinator towards the un-pollinated (yellow) flowers. The retention of pollinated (red) flowers in the inflorescence also makes flowers appear more beautiful from a distance.

Floral Scent

Many flowering plants’ reproductive biology depends heavily on floral fragrance (Harborne, 1993) [20]. Plants that are pollinated by a range of animals, including birds, bats, beetles, butterflies, moths, bees, and wasps, will be attracted by scents. The existence of rewards for foraging pollinators, like as nectar or pollen, or momentary protection from predators, will be announced by scent. Gene expression, biosynthesis, and occasionally degradation have a role in the
creation of volatiles, and these processes fluctuate quickly during the day. Additionally, the rate of volatile emission rises with temperature and/or light, and the wind aids in the spread of these gases. Therefore, flower aroma can indicate in much more ways than colour, form, or texture. Floral volatiles are not only proximal and distal attractants of mutualistic pollinators (Kessler et al., 2008; Larue et al., 2015) [25, 31]; they also deter florivores, nectar and pollen thieves, and protect floral organs against bacteria and yeasts.

Pollination and Floral Volatiles
According to Harborne (2001) [21], the floral volatiles are crucial in drawing pollinators to the plant. They might draw a wasp or bee that helps with pollination from a few metres away. Beetles are attracted to fruity or aminoid aromas, while bees, moths, butterflies, bats, and dung-flies are drawn to sweet smells. Low molecular weight and high vapour pressure molecules make up floral fragrance, which diffuses throughout the environment to inform pollinators where the blooms are located. Terpenoids, benzenoids, and phenylpropanoids (derived from phenylalanine), as well as green leaf volatiles (GLVs) generated from fatty acids, are the main types of volatiles released by flowers (Muhlemann et al., 2014) [33]. Typically, the floral aroma is produced at the ideal time of day for the specific pollinator, such as during the day for flowers that are pollinated by bees. For species that are pollinated by moths, it can be at sunset or even later in the evening.

<table>
<thead>
<tr>
<th>Floral volatiles</th>
<th>Plant species</th>
<th>Pollinator</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dimethyl trisulfide (24.3%), dimethyl disulfide, dimethyl tetrasulfide, etc.</td>
<td><em>Crescentia cujata</em></td>
<td>Bat</td>
</tr>
<tr>
<td>Squalene (26.5%) nerol, geraniol, hydrocarbons</td>
<td><em>Dactylanthus taylorii</em></td>
<td>Bat</td>
</tr>
<tr>
<td>Geraniol, citral, farnesol, etc.</td>
<td><em>Catasetum maculatum</em></td>
<td><em>Eulaena</em> male bee</td>
</tr>
<tr>
<td>Carvone oxide</td>
<td><em>Daphne mezereum</em></td>
<td><em>Colletes</em> bee</td>
</tr>
<tr>
<td>Linalool (95%) - its oxides</td>
<td><em>Cucurbita</em> spp.</td>
<td><em>Diabroticite</em> beetle</td>
</tr>
<tr>
<td>Indole, 1,2,4 trimethoxybenzene, cinnamaldehyde</td>
<td><em>Cimifuga simplex</em></td>
<td>Butterfly</td>
</tr>
<tr>
<td>Methyl anthranilate and isoeugenol</td>
<td><em>Platanthera chlorantha</em></td>
<td>Moth</td>
</tr>
<tr>
<td>Methyl benzoate (25%), linalool (50%), geraniol (12%)</td>
<td><em>Zygogynum</em> spp.</td>
<td>Moth</td>
</tr>
<tr>
<td>Ethyl acetate, monoterpenes, and aliphatics</td>
<td><em>Brugmansia x candida</em></td>
<td>Hawkmoth</td>
</tr>
<tr>
<td>trans-Ocimene (50% (46%), 1,8-cineole (12%)</td>
<td><em>Andrena</em> male bee</td>
<td>Diadromus* bee</td>
</tr>
<tr>
<td>Heptan-2-one (16%), indole (16%), germacrene B (49) (18%), p-cresol (3%)</td>
<td><em>Arum maculatum</em></td>
<td>Dung-fly</td>
</tr>
</tbody>
</table>

Source: Abrol, 2012 [1].

In the angiosperms, a flower's aroma or perfume frequently plays a significant role in luring pollinating insects. Many of the flowers that attract bees, such as the garden violet and other Viola species, have odours that we would describe as fragrant or 'heady', and the bees are particularly attracted to these aromas. Odour is particularly important to species that fly at night, since visual stimuli are nearly non-existent; bat- and moth-pollinated flowers typically have powerful aromas. Flower scents are presumably effective at relatively low quantities since insects are sensitive to modest concentrations of volatile compounds. Many species, even those that don't seem to have strong scents to human senses, may actually create enough fragrance to draw bees or butterflies. In many species, the peak smell production often coincides with the flower's pollen ripeness and pollination readiness. Additionally, production varies throughout the day; smell is created about midday for daytime pollinators and at dusk for nighttime pollinators.

In-depth research has been done on how plants use these aromas to lure insects into their traps (Faeqri and van der Pijl, 1979) [14]. For instance, the vivid purple spathe of *Arum nigrum* and *A. vnaucula* opens overnight to reveal the spadix, where respiration is extraordinarily rapid and temperatures of 30 °C have been recorded. By creating heat in the spadix in this way, the amine is more easily converted into the offensive odours that are then emitted. The amine draws dung beetles and flies, which land on the spadix and drop to the flower's base where they are hatched. The slippery inner spathe surface prevents the insects from escaping, so they remain imprisoned for 24 hours while they transfer pollen to the receptive styles. After this period, rapid anatomical changes (including wrinkles in the spathe surface) take place, and the insects are eventually freed.

Flower Scents mimic Insect Pheromones
Since insects rely on volatile substances for social interaction, it stands to reason that they could develop a sensitivity to the same chemicals found in, say, flower smells. Plants occasionally trick insects by emitting enticing scents to catch them or distract them from more lucrative activities (like feeding, for example).

Vereecken and Schiestl (2009) [45] documented that by imitating the mating signals of female insects, typically hymenopterans, sexually deceptive orchids are able to cross-pollinate (Fig. 6). Due to its primary foundation on the imitation of mating signals, particularly the female sex pheromone of the targeted pollinator, this pollination process is frequently quite selective. Male bees pollinate three varieties of the orchid *Ophrys insectifera* by engaging in pseudo-copulation with flowers that resemble female bees in morphology, colour, and scent. The involvement of many species of male bees raises the possibility that there are various floral scents.

![Fig 6: Orchid (*Ophrys* spp.) pollination through mimicking the mating signals of female insects (*Andrena* bee)](https://www.biochemjournal.com)
Thermogenecity’s Effect on the Release of Odours
Heat is a byproduct of metabolic biochemical activity, which is present in all known flowers (Seymour and Schultz-Motel, 1997) [42]. However, because the reaction that generates heat in the majority of flower-producing plants is sluggish, the heat dissipates gradually. On contrary, the plants that are properly categorised as “thermogenic” create an exceptionally high amount of heat in a remarkably short length of time. According to Seymour and Schultz-Motel (1997) [42], this considerable heat output is not thought to be a byproduct of metabolic activity but rather is created to fulfil some ecological need or function. Even these plants’ episodic heat generation typically coincides with the time when the female flower parts are most amenable to pollination and the floral aroma is most potent (Seymour and Schultz-Motel, 1997) [42].

In order to draw the beetle pollinator, Cyclocephala atricapilla (Coleoptera: Dynastidae), Annona coriacea has a thermogenic function (Gottsberger, 1990) [16]. It appears that this plant can grow a useful blossom that warms to 34 °C, which may be up to 15 °C higher than the surrounding air temperature. The goal of this thermogenesis is once again to volatilize a distinctive spicy scent that draws the beetle for pollination.

According to Gottsberger (1990) [16], the Philodendron selloum (Araceae) has a thermogenic function. Thermogenesis takes place in the evening and can reach temperatures of 46 °C, which could be up to 30 °C higher than the surrounding air temperature. However, Philodendron selloum is one of the rare plant species that has been seen to exhibit lipid oxidation during the first heating phase, an abnormality from normal starch utilisation. Eriocelis emarginata (Dinastidae), the plant’s representative beetle pollinator, is attracted over considerable distances by its very distinctive respiration process and the heat it generates. It is not uncommon for 50, 100, or even 200 beetles to be seen concurrently approaching a single inflorescence due to the inflorescence’s strong attractivity (Gottsberger, 1990) [16].

Floral Rewards: Nectar and Pollen
Nectar constituents
The nectar is one of the key reasons why animals visit flowers, and most pollinators depend on it for nutrition, especially those like butterflies who don’t have access to other food sources. It is obvious that nectar serves no use other than to draw pollination animals to angiosperm flowers. Nectar contains toxins that keep out unwelcome guests (Kessler et al., 2008 & 2012) [25-26], as well as carbohydrates, amino acids, and volatile chemicals that draw and reward pollinators (De la Barrera and Nobel, 2004).

Sugars of Nectar
The majority of nectars that have been studied are just a sugar solution. Most of them taste extremely sweet and range in sugar concentration from 15% to 75% by weight. The three common sugars used by plants in their metabolism, glucose, fructose, and sucrose, are present as compounds. Numerous plant nectars include oligosaccharides as well, though usually in minute amounts. The trisaccharide raffinose (6G-galactosylsucrose) is the most prevalent of these and can be found in nectars of related families including Berberidaceae and Ranunculaceae.

There are considerable quantitative variances between species, according to a survey of the three common sugars in nectars among over 900 species (Percival, 1961) [36]. In fact, there are three main categories of angiosperm nectars: those in which sucrose predominates (such as those from Berberis and Helleborus), those in which all three sugars are present in roughly equal proportions (such as those from Abutilon), and those in which glucose and fructose predominate (such as those from crucifers, umbrellifers, and other composites). These findings support the hypothesis that the angiosperms have evolved from nectars containing primarily sucrose to those containing primarily glucose and fructose.

According to Baker and Baker’s (1990) [3] investigation of nectar types, the kind of pollinator that visits the flower and the ratio of sugars present are related (Table 3). This is most noticeable in the genus Erythrina, where flowers that are pollinated by passerine (perching) birds are consistently high in glucose and fructose, but blooms that are pollinated by humming birds are high in sucrose. Such correlations may, in some circumstances, be utilised to identify potential plant pollinators.

Table 3: Relationship between nectar classes and pollinator types

<table>
<thead>
<tr>
<th>Sugar ratio</th>
<th>Pollinators</th>
</tr>
</thead>
<tbody>
<tr>
<td>High sucrose (&gt;0.5), e.g., average for 27 species of passerine bird-pollinated Erythrina = 1.3</td>
<td>Big bees; Humming birds; Lepidoptera</td>
</tr>
<tr>
<td>Low sucrose (&lt;0.5), e.g., average for 23 species of passerine bird-pollinated Erythrina = 0.04</td>
<td>Small bees; Passerine birds; Neotropical bats</td>
</tr>
</tbody>
</table>

Amino Acids of Nectar
According to Gardener and Gillman (2008) [15], amino acids are the second-most prevalent type of chemical (after sugars) in nectar and are crucial in shaping the foraging preferences of pollinators. Nectars contain all of the common protein amino acids (Baker and Baker, 1975) [9]. Baker (1977) [7] documented that nectars from flowers pollinated by insects such as settling moths, butterflies, and many wasps were shown to be more abundant in amino acids. These insects lack alternate sources of protein-building elements as adults. In contrast, flowers that are pollinated by bees have lower levels of amino acids since they can get their nitrogen from other sources (such as pollen).

In fact, a correlation between an increase in amino acid content and an increase in evolutionary development was found (Table 4), with woody primitive families typically having lower amino acid scores than advanced herbaceous groupings. This is also related to the fact that bees, who may receive nitrogen from other sources (such as pollen), typically pollinate the lower scoring groups. In contrast, the families with higher scores have a disproportionately higher number of species that are pollinated by butterflies and, to a lesser extent, moths (Table 5).
Nectar Toxins
Toxins that are perhaps derived from their manufacture in other plant sections may be present in plant nectars. Although several other classes have also been reported, alkaloids have been found most frequently. Although the function of toxin buildup in nectars is yet unknown, it is possible that it serves as a defence mechanism against herbivores or unwanted animal visitors. According to Stephenson (1982) [43], the Catalpa speciosa plant produces iridoids in its nectar as a defence against ants, which are known nectar thieves. Occasionally, certain butterflies may gather the toxins in the nectar while they pollinate a plant. Adult Ithomines and Danaids, which depend on pyrrolizidine alkaloids for both defence and pheromone generation, are examples of this. These alkaloids are derived from the nectar of Senecio and Eupatorium species, which are raised in the appropriate environments.

Pollen Constituents
Around 140 million years ago, during the Cretaceous period, pollen may have served as the first incentive (bribe) to draw insects to flowers. Like nectar, pollen is a highly nutritious and well-balanced food source that includes protein, sizeable amounts of starch, sugar, fat, and antioxidants as well as vitamins like thiamin. It also contains a lot of free amino acids. Many flower visitors collect and use the pollen because it is typically easier to get than the nectar. Bees and beetles in particular collect and consume pollen. Pollen is frequently coloured, particularly by carotenoid pigments but also by flavonoids, and this is likely a signal to advertise to insect feeders that the pollen is available. Pollen typically contains the carotenoids like α and β carotene, lutein, zeaxanthin and their different epoxides. Anthocyanidin serves as the colour in many types of pollen that are dark red or purple, like Anemone. Pollens usually include additional flavonoids, particularly the flavonol isorhamnetin, which gives them their pale yellow hue. Since pollen serves as the major vehicle for male gametophytes, hence any use of it by animals for food is secondary and represents pollen theft as far as the plant is concerned. Since the majority of angiosperms produce too much pollen, there is rarely a conflict between the two different uses of pollen. Pollen would be wasted if insects did not make use of the extra that was available to them.

Rewards (Floral oil): Other than nectar and pollen
Lipids and their constituent fatty acids contain more energy per unit of weight than sugars, so a plant may benefit from using this nutritional attractant instead of sugar as less needs to be produced. A similar substitution has happened during the evolution of angiosperms, but it seems to have happened rather infrequently. Indeed, lipids were only recently acknowledged as nectar constituents, after Vogel's (1969) [46] finding of them in a small number of Scrophulariaceae species that are pollinated by bees. Lipids have since been discovered in animals spanning 49 genera and five Families. These include the Orchidaceae, Iridaceae, Krameriaceae, and Malpighiaceae in addition to the Scrophulariaceae (Vogel 1974) [47]. Certain species of solitary bees of the Anthophoridae, which serve as pollinators for the aforementioned plants, seem to be directly tied to lipid biosynthesis. Although it has been seen that adult male bees also consume the oil, the oil is mostly used by the bees to feed their young. In Centris species, only the female is capable of collecting it. She then brings it back to the nest, combines it with pollen, and lays an egg on the mixture. When the eggs hatch, the young are given a special, lipid-rich meal to grow on. Thus, these lipids have an impact on the co-evolution of plants and pollinators. The plants gain from the bees' faithful pollination, while the bees profit from a diet high in energy. There haven't been many chemical analyses of nectars that contain lipids, thus it's unclear whether they often contain triglycerides of the common variety.

Table 4: Amino acid concentration of nectars according to plant family

<table>
<thead>
<tr>
<th>Relative advancement</th>
<th>Plant family</th>
<th>Total amino acid on histidine scale</th>
</tr>
</thead>
<tbody>
<tr>
<td>More</td>
<td>Asclepiadaceae</td>
<td>8.4</td>
</tr>
<tr>
<td></td>
<td>Liliaceae</td>
<td>7.4</td>
</tr>
<tr>
<td></td>
<td>Campanulaceae</td>
<td>7.0</td>
</tr>
<tr>
<td></td>
<td>Leguminosae</td>
<td>6.9</td>
</tr>
<tr>
<td></td>
<td>Amaryllidaceae</td>
<td>6.9</td>
</tr>
<tr>
<td>Less</td>
<td>Compositae</td>
<td>6.3</td>
</tr>
<tr>
<td></td>
<td>Rosaceae</td>
<td>3.9</td>
</tr>
<tr>
<td></td>
<td>Myrtaceae</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td>Saxifragaceae</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>Caprifoliaceae</td>
<td>2.2</td>
</tr>
</tbody>
</table>

Source: Baker and Baker, (1973) [40]

Table 5: Amount of amino acid in nectars of plants with different animal visitors

<table>
<thead>
<tr>
<th>Animal group</th>
<th>Amount of amino acid on histidine scale</th>
<th>Other sources of nitrogen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carrion and dung flies</td>
<td>9.0</td>
<td>None, flowers mimic carrion or dung</td>
</tr>
<tr>
<td>Butterflies</td>
<td>5.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Pollen not eaten</td>
</tr>
<tr>
<td>Moths</td>
<td>5.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Pollen eaten</td>
</tr>
<tr>
<td>Wasps</td>
<td>5.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Ingest large amounts of nectar</td>
</tr>
<tr>
<td>Bees</td>
<td>4.6</td>
<td>Insects eaten</td>
</tr>
<tr>
<td>Birds</td>
<td>3.9</td>
<td></td>
</tr>
<tr>
<td>Bats</td>
<td>3.6</td>
<td></td>
</tr>
</tbody>
</table>

Source: Baker and Baker, (1986) [40] and Abrol, (2012)[1]
Effects of herbivore-induced plant volatiles on interactions between plants and pollinators

Plants must choose between protecting themselves from environmental pressures and pursuing growth, development, and reproduction. Plants have developed a wide range of inherent and induced defence mechanisms against predators, including the systemic release of herbivore-induced plant volatiles (HIPVs). Despite the fact that herbivory is known to alter flower features in a number of plant species, including size, nectar secretion, and composition, studies addressing both HIPVs and pollinator behaviour are uncommon.

In most cases, however (Adler et al., 2001; Cardel and Koptur, 2010; Danderson and Molano-Flores, 2010) [2, 8, 11], folivory and florivory reduced pollinator visitation. In comparison to plants afflicted with herbivores, bees and syrphid flies visited unharmed wild radish plants more frequently (Lehtilä and Strauss, 1997) [32]. Fewer and smaller flowers were blamed for the lesser preference for bees that was observed. However, there was no correlation between changes in the measured morphological floral features and syrphid fly preference. These results imply that the syrphid flies may have distinguished between damaged and healthy plants using chemical cues.

The foraging behaviour of pollinators is influenced by plant smells (Kessler and Halitschke, 2007; Kessler and Baldwin, 2007; Raguso, 2008) [23, 27-28], and further research is needed to determine whether HIPVs are responsible for the reported alterations in pollinator behaviour (Dicke and Baldwin, 2010; Kessler and Halitschke, 2007) [23, 27]. Recently, research has focused on figuring out how changes in the olfactory cues released by flowering plants that have suffered herbivore damage can affect pollinator behaviour. There were no observed effects of flower quantity, display, or reward quality on pollinator behaviour for Cucurbita pepo subsp. texana plants. However, once the leaves were mechanically injured, pollinator visitation decreased in response to changes in the volatile emission rate of the flowers (Theis et al., 2009) [44]. When an insect herbivore damaged the leaves on wild tomato plants, pollinators visited those plants less frequently and spent less time there (Kessler and Halitschke, 2009) [24]. Wild tomato plants that had Manduca sexta caterpillar injury on their leaves produced dramatically different floral volatile emissions than unharmed plants. These findings suggest that systemic and local HIPV emission may alter pollinator foraging behaviour, and that when pollinator visitation is negatively impacted, this puts pressure on HIPV emission through a negative selection process (Dicke and Baldwin, 2010) [12].

Conclusions

The importance of flower colour, floral aroma, nectar, and pollen has each been discussed in turn in this review to cover the various biochemical components of plant pollination. All these elements could combine in specific plant-pollinator interactions in the field. In some interactions, one or more biochemical factors may predominate, whilst in others, nectar, flower colour, and scent may all be necessary to draw a specific pollinator.

While the primary function of a flower's colour, fragrance, and floral reward is to draw in a pollinator who is already there, it is important to keep in mind that plants also need to defend themselves from outside visitors who might take the floral reward without pollinating the flower. Thus, both appealing and repelling visitors may depend on biochemical (and structural) characteristics. Bees, for instance, are not typically attracted to red blooms because they are intolerant to this colour. They also avoid plants whose nectar contains sugars that they are unable to digest, such as mannose.

One last idea is the dynamic nature of the link between flower and pollinator, which is demonstrated here by a number of examples. The environment is constantly evolving, and certain relationships that appear to be closely bound (such the links between bees and orchids and wasps and orchids) may be subject to change.

References


43. Stephenson AG. Toxic nectar deters nectar thieves of Catalpa speciosa ... speciosa are unpalatable to nectar thieves. Journal of Chemical Ecology. 1982;8:1025-1034.


