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PERSPECTIVE

Flowers and Fungi Use Scents to Mimic Each Other

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Some flowering plants mimic the scent and appearance of mushroom fruiting bodies. Fungi may also mimic flowers. In addition, infection of plants by certain fungi can direct the plant to develop nonfunctional floral-like structures that nonetheless primarily serve the reproductive advantage of the fungus. These various mimicries may serve to attract insects that in turn spread fungal spores or plant pollen, thus facilitating sexual reproduction of the cryptic organism.

The ultimate purpose of the scent of a flower, in conjunction with its shape and coloring, is to attract the respective pollinators to ensure the preservation of the species. Some of these scents are delightful, as for night-scented moth flowers. Others are putrid, as for flowers that mimic carrion or dung to attract certain fly species that deposit their eggs in the flowers, thereby acting as pollinators. The interchange serves only the flower, however, as the fly larvae usually cannot develop. Such so-called sapromyophilous flowers occur in primitive as well as in highly advanced angiosperms (*1*).

Fungus gnat flowers also attract flies to their flowers. They mimic the fruiting bodies of mushrooms by scent and morphological appearance. Fly species that normally deposit their eggs in mushrooms are attracted to these flowers and thus pollinate them. Flowers of the genera *Asarum* and *Aristolochia* (Aristolochiaceae), *Arisarum* and *Arisaema* (Araceae), and *Dracula* (Orchidaceae) use this strategy (*2*).

The extraordinarily shaped flowers of *Dracula chestertonii* (Fig. 1), native to the Colombian Andes, emit a mushroom-like scent assumed to attract females of a fungus fly species. The large lip imitates the lamellated cap of fungi so well that the fungus fly deposits its eggs in the fake mushroom cap and incidentally effects pollination of this orchid (*2*). The floral fragrance of *D. chestertonii*, which corresponds to what people recognize as champignon scent, includes the typical mushroom constituents oct-1-en-3-ol (**1**), oct-1-en-3-one (**2**), octan-3-ol (**3**), and octan-3-one (**4**), making up more than 70% of the volatiles (*3*, *4*) (Fig. 2). The flowers of the orchid *D. vampira*, endemic to Mount Pichincha in Ecuador, also emit a mushroom scent of comparable olfactory quality to *D. chimaera*.

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Another fascinating example of a fungus gnat flower is that of *Aristolochia arborea*, a small tree from the rainforest of Central America (*2*). The flowers appear at the base of the stem in short branched inflorescences. The perianth forms a flytrap typical of Aristolochiaceae. These flowers present a perfect imitation of a small toadstool in the center of the brown perianth tube. The "toadstool" resembles a member of the genus *Marasmius* (*5*), fungi that grow in tropical rainforests. The flowers of *A. arborea* emit a rather faint meaty, earthy, and mushroom-related scent. Because of the very low scent emission, we have so far been able to identify only the main constituents of the floral scent of *A. arborea*: the terpenoids α-pinene, camphene, β-pinene, sabinene, limonene, β-cedrene, caryophyllene, germacrene D, bicyclogermacrene, germacrene A, and germacra-1(10),5-dien-4-ol.

Fungi, just as flowering plants, may use mimicry to steal resources to ensure survival. An impressive example is that of the witches' brooms on *Berberis vulgaris*, which are induced by the systemically infecting rust fungus *Puccinia arrhenatheri* (*6*). *B. vulgaris* is the alternate host of *P. arrhenatheri* and at least five other *Puccinia* spp., the wheat rust (*P. graminis*) included, which all infect grass species as their primary host. Thus, barberry shrubs are eradicated in areas with intensive wheat cultivation. During the spermatic stage of *P. arrhenatheri*, the infected leaves of *B. vulgaris* reveal a yellowish color, reminiscent of flower petals, and emit a strong floral-fruity and herbaceous scent, which is mainly due to indole (**5**), methyl nicotate (**6**), carvacryl methyl ether (**7**), (*Z*)-7-decen-5-olide (**8**, jasmine lactone), (*Z*)-7-decen-4-olide (**9**, γ-jasmolactone) (*6*), and its precursor (*E*,*Z*)-5,7-decadien-4-olide (**10**) (Fig. 3). Of these, only traces of indole were found in the uninfected leaves, which give off no more than 2% of the quantity of volatiles given off by either infected leaves or flowers. The bright yellow color and the strong scent of infected leaves mimic flowers and attract a wide diversity of insects, which facilitate the sexual reproduction of the pathogen by transporting spermatia (*6*).

Fungal infection inhibits the barberry shrub from blooming. The flowers of uninfected *B. vulgaris* open later in the season, when the fungus has terminated the production of spermatia. By contrast to the flowery-fruity fragrance of witches' brooms, *B. vulgaris* flowers emit a peculiar spermy odor even though it is based on pleasant odorants such as linalool and isomers of lilac aldehyde and lilac alcohol (*6*). The spermy odor aspect frequently encountered in flower scents is due to minor amounts of 1-pyrroline (**11**) and traces of 2-acetyl-1-pyrroline (**12**) (Fig. 3).

Another fascinating example of floral mimicry by a plant pathogenic fungus is the systemic infection of the Canada thistle *Cirsium arvense* by the fungus *P. punctiformis* (*7*). During its spermatial stage, the fungus on the infected thistle shoots emits a strong floral scent that is mainly based on phenylacetaldehyde, 2-phenylethyl alcohol, and indole.

Floral mimicry can address both scent and shape so much that it convinces even the human eye. Rust fungi in the *P. monoica* complex infect 11 species of Brassiaceae, mainly North American *Arabis* species, modifying host leaf morphology to produce fungal "pseudoflowers" that aid the sexual reproduction of the fungus (*8*). "Pollinator" attraction is accomplished through visual floral mimicry, the presence of nectar reward, and floral fragrances. The pseudoflower scent does not appear to represent a simple modification of host floral or vegetative emission, nor does it mimic the scent of co-

Fig. 1. The unusually large flower lip of *Dracula chesteronii* (Rchb.f.) Luer, an orchid native to the Colombian Andes, mimics by scent and appearance the fruiting body of a mushroom to attract fungus gnats (width of lip, 2.5 cm).

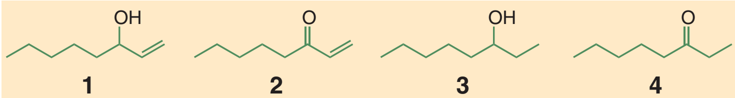

Fig. 2. Typical mushroom constituents dominating the flower scent of *Dracula chestertonii* (Rchb.f.) Luer.

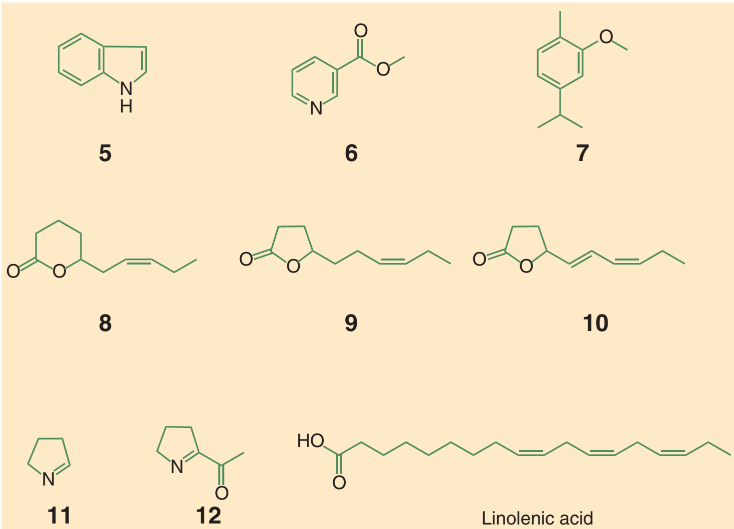

Fig. 3. Typical scent constituents emitted from pathogen specimens of *Berberis vulgaris* L., *Euphorbia cyparissias* L., and *Euphorbia verrucosa* L.

Fig. 4. Flowering plants of *Euphorbia cyparissias* L. together with specimens infected by a rust fungus of the species complex *Uromyces pisi* and having developed so-called pseudoflowers (width of rosette, 1.5 cm).

blooming flowers. Instead, the unique fragrances, beyond their function as pollinator attractants, may reduce gamete loss by reinforcing constancy among foraging insects (*9*, *10*). The distinct scent of these fungal pseudoflowers is composed primarily of aromatic compounds such as 2-phenylethyl alcohol and its esters as well as phenylacetaldehyde (*10*), compounds also found in thistle when infected by *P. punctiformis* (*7*).

Impressive pseudoflowers, yellow leaves that grow in a dense terminal rosette and resemble true flowers in color and shape (*11*) (Fig. 4), are also formed by the systemic infection of *Euphorbia cyparissias* by rust fungi of the species complex *Uromyces pisi*, the latter being common pathogens of *E. cyparissias* in Europe (*12*). Like true flowers, they present scent and sweet-smelling nectar on the surface, which contains fungal gametes that are transferred by nectar-feeding insects from one fungal mating type to the other (*11*). The true flowers of *E. cyparissias* are characterized by a green, aromatic-floral, honey-like odor mainly consisting of mono- and sesquiterpenes, lipid metabolites such as (*Z*)-hexen-3-yl acetate, and aromatic compounds including phenylacetic acid. By contrast, the scent given off by rust-induced pseudoflowers is distinct and variable, most likely depending on the taxonomic affiliation of the fungal parasite and perhaps also on the maturity of the pseudoflower.

We found that pathogen specimens from Oberstammheim (northeast Switzerland) had a strong spermy scent containing at least 30% 1-pyrroline (**11**), but those near Birchwil (northeast Switzerland) and in other habitats had the fruity-floral scent of peach, mainly caused by jasmine lactone (**8**) and indole (**5**) (Fig. 3). To make it even more complicated, other *Euphorbia* species may be infected by *Uromyces* species and develop similarly looking pseudoflowers. Near Merishausen (northeast Switzerland), *E. cyparissias* co-occurs with *E. verrucosa*, but only the latter species was infected and developed pseudoflowers induced by *U. euphorbiae-Craccae* (*12*), which emitted again a distinct floral-fruity scent, this time dominated by a new scent compound of molecular weight 168. We isolated this compound and elucidated its structure by nuclear magnetic resonance as (*E*,*Z*)-5,7-decadien-4-olide (**10**), the biological precursor of the widespread (*Z*)-7-decen-4-olide (**9**). Structural considerations suggest that **10** as well as **9** and the δ-analog **8**, including derivatives, are biogenetically derived from linolenic acid. In fact, the lactones **10** and **9** are formed from linolenic acid by biodegradation (*13*). Linolenic acid is metabolized, probably by *U. euphorbiae-Craccae*, in pseudoflowers of *E. verrucosa* mainly to γ-lactones (e.g., **10**, **9**) and in those of *U. pisi s. lat* on *E. cyparissias* exclusively to δ-lactones (e.g., **8**), whereas *P. arrhenatheri* on *B. vulgaris* (*6*) activates both pathways.

The olfactory mimicry that these fungi and flowers use to their advantage coincidentally produces scents that elicit strong human reactions, whether of disgust or delight. We choose the latter as the base for new perfumes.

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