Chapter 5
Medicinal and Aromatic Plants (MAP): How Do They Adapt to the Environment?

A. Cristina Figueiredo and José G. Barroso

Abstract Taking the best out of plants, namely from medicinal and aromatic plants (MAP), involves understanding their structural and chemical features, in connection with their biological roles, and, no less important, realizing the principles behind their use by plants. Plants are exquisitely sensitive to biotic and abiotic environmental changes. Nevertheless, plants are unique in their renewal capacity, since they can produce meristems during their life time, and in showing developmental plasticity, i.e., the ability to change its development in response to diverse factors. This means that a plant can very often survive, despite having been partially eaten, and/or that a single plant genotype can be expressed under different phenotypes, and the one(s) expressed will depend on local environmental stimuli. From man point of view this may have importance, as these different phenotypes can be associated to different chemotypes, which may have a tremendous implication on the biological activity of plant man-valued products and on their commercial value. Some of the structural and chemical traits involved in plant-abiotic and plant-biotic defence, and in attraction interactions, with some examples on how man uses some of these traits and mechanisms to his benefit, are here revised. Apoplastic barriers, glandular or non-glandular structures, mimicry, plant, or plant parts, movements, abiotic environmental relationships, interaction with pathogens and phytophagous and attraction of pollinators and seed dispersers, are discussed. In each case, plants use both constitutive, as well as inducible traits. Nevertheless, it is noteworthy that constitutive traits are not always constant. Indeed, constitutive structural and chemical features can be permanent or transient, depending on the plant developmental stage. Despite all available traits, plants are endowed with self-defence mechanisms against their own toxins. The awareness of plant structural and chemical adaptative features purposes can complement the knowledge derived from evolutionary studies, and provide us the know-how to project and develop plants with improved traits, or procedures based on their *modus operandi* and/or better plant (nano-)products.

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Á. Máthé (ed.), *Medicinal and Aromatic Plants of the World*, Medicinal and Aromatic Plants of the World 1, DOI 10.1007/978-94-017-9810-5_5

Keywords Medicinal and aromatic plants • MAP • Abiotic • Biotic • Structural features • Chemical features • Self-defence features

1 Introduction

Since ancient times plants have played a major role as food providers and as a physical and mental healing source. For their ornamental value, or for their use in horticultural therapy (Adevi and Lieberg 2012), they are known to reduce stress and improve well-being. However, many plants are toxic and they are used in particular socio-cultural contexts, namely as a tool for hunting, or fishing, or in rituals of superstition and magic. But human beings rely on plants for many beneficial effects and commodities. Plants provide many food and non-food products, including cloths, wood, dyes, cosmetics, and medicines, among many others products, or they serve as raw material for diverse commercial and industrial fine chemicals.

Medicinal and aromatic plants (MAP) embrace a diversity of such species, that have in common producing a wide range of natural compounds important to man and animals. Although many plants combine both the aromatic and medicinal properties, not all possess this dual characteristic. There are numerous examples of non-aromatic plants that produce active principles having valuable pharmacological properties, such as, for instance, foxglove (*Digitalis* spp.), whereas others are essentially known and used for their valuable aroma, such as jasmine (*Jasminum* spp.) (Barata et al. 2011).

Throughout the world, there is an ever-increasing interest in MAP, regarding their use, development, cultivation, conservation and sustainable use, as they are of utmost economic and social importance. These plants are also targets for several studies on pharmacognosy, phytochemistry, ethnobotany and biology. In addition to their medicinal value and to being traded as regular commodities, new trends of their use for sauces or jam production, or for flavouring olive oil, vinegar, wine, chocolate, wood, honey, paper or soap, reveal their enormous importance for local and countries' economies (Barata et al. 2011). Nevertheless, the production of MAP, and derived products are not always stable. Being biological systems, they can be negatively affected by many factors occurring prior to- or after harvest, namely natural catastrophes, phytophagy, storage, extraction mechanisms, to name just a few (Figueiredo et al. 2008a).

Given, in most cases, the close relationship between the metabolites produced by-, or the structural adaptations present in, plants and their surroundings, the knowledge on how plants react has important practical applications. Let us not forget that many man used products derived from plants are used by the plant either to deter phytophagous or to attract pollinators. This means that several of these products have some level of toxicity and their action is very much dose-dependent. As a consequence they may, if not correctly used, have negative implications on those using-, or working with them, independently of the route of administration (local or systemic).

So as to know the factors that influence MAP productivity, it is thus important to understand how a plant reacts and adapts to environmental biotic and abiotic challenges. Several studies on the factors affecting volatile components and essential oils production in plants, showed that the response is species specific (Figueiredo et al. 2008a). This chapter deals with medicinal and aromatic plants strategies to adapt to the surrounding environment, and how man has taken, or can take, advantage from these mechanisms.

2 Biological Importance of MAP Adaptation

"We must consider the distinctive characters and the general nature of plants from the point of view of their morphology, their behaviour under external conditions, their mode of generation, and the whole course of their life" [Theophrastus (372–287 B.C.) (transl. A. G. Morton 1981)].

Indeed, as plants are unable to move, they must rely on their morphology and on a variety of strategies to tolerate adverse biotic or abiotic conditions and to interact with pollinators, or otherwise they will perish, either because they will not endure the hostile environment or because they will not be able to propagate.

Plants interact with the environment for one of two reasons: defence from biotic and abiotic factors and/or attraction of pollinators and seed dispersing animals, Table 5.1. In each case, plants use both (a) constitutive, i.e. always present, and (b) inducible, i.e. activated by external factor, physical and chemicals traits. Chemical constitutive traits, as well as some physical ones, can be permanent, or transient, that is, vary with flowering stage, plant age, or other physiological factors (Figueiredo et al. 2008a). Moreover, chemicals involved in plant interactions can both be derived from (a) primary-, i.e. directly involved in growth, development, and reproduction, and/or (b) secondary metabolism, i.e. mostly having an ecological role (Figueiredo et al. 2008a). Nevertheless, it is important to stress that plant interactions rely on all mechanisms, physical and chemical, combined; there is not real boundary that clearly separates them, and they together act as a whole in the plant response.

2.1 *Defence from Abiotic and Biotic Factors*

Plant biomass yield can be severely affected by high winds, flooding, drought, high or low temperatures, high salinity, inadequate light intensity or nutrients concentration, pollution, amid other abiotic factors (Figueiredo et al. 2008a). Moreover, plants are surrounded by mammals, birds, insects, as well as nematodes, bacteria, viruses, fungi, among others. But if plants depend, in some cases, on some of the living organisms surrounding them, for pollination and seed dispersal, they have also to protect themselves from phytophagous and pathogens. Although the plant

Table 5.1 Structural and chemical mechanisms involved in plant-abiotic and plant-biotic defence and attraction interactions

Defence from abiotic and biotic factors
Structural features
Apoplastic barriers
Glandular or non-glandular structures
Mimicry and plant, or plant parts, movements
Chemical features
Relationship with the abiotic environment
Interference in community development (allelopathy and semiochemicals)
Interaction with pathogens and phytophagous
Attraction of pollinators and seed dispersers
Structural features
Chemical features

resistance or sensitivity is very much plant-specific, depending, *inter alia*, on the genotype and plant physiological stage (Figueiredo et al. 2008a), there are several structural and chemical features that help plants in their abiotic and biotic interactions.

2.1.1 Structural Features

The effect of fire, over-radiation and heat, grazing, pathogen attack, herbivory, for instance, can be mitigated in several ways by physical barriers. Among these, both constitutive and inducible structural features, the (a) apoplastic barriers, (b) glandular and non-glandular structures, and (c) mimicry and movements will be point out.

Apoplastic Barriers

In addition to cellulose and lignin, other classes of compounds, such as cutin, waxes, suberin, silica or callose, provide major plant surface physical (as well as chemical) protection. The outer cell walls of the epidermis of plants aerial parts are coated with a multilayered structure, of variable thickness, the cuticle, mainly composed of the hydrophobic cutin and waxes. In addition to its natural hydrophobic nature, waxes may show a coarse microstructure that enhances water repellence. The cuticle regulates the degree of surface hydration, the emission of volatiles, and protects, for instance, from rainwater leaching, wind erosion, abrasive moving soil, the action of pollutants and infections.

Combining a hydrophobic wax coating with structural roughness (nanostructures), the water-repellent lotus (*Nelumbo nucifera*) leaves, are known to be superhydrophobic, self-cleaning, and antifouling, known as the Lotus-effect

(Hsu et al. 2011; Bhushan 2012). The cuticle from lotus leaf epidermal cells possesses epicuticular wax protuberances, papilla, responsible for the structural roughness. Water droplets stand on the top of these nanostructures surface because air bubbles fill the gaps between them. The self-cleaning effect is of great importance for plants as allows the non-dirty surface to be available for photosynthesis and avoids pathogen contamination.

Suberin can occur not only internally, at the Casparian strip of the root endodermis, but it is also associated with the cork cells of the periderm, forming the outer bark of stems and roots of many species. The presence of this very thick and insulating bark, the cork, has a protection role on *Quercus* suber (cork oak) buds, enabling them to resprout after fire (Pausas et al. 2008). The knowledge on the factors that enable fire resistance and resilience are extremely important in correct forest management policies.

Stinging nettle (*Urtica dioica*), sometimes used as medicinal plant, is an example of a higher plant that possess cells with silica mineralized cell walls. The stinging trichomes (definition below), consist of a single narrow and long cell that ends in small bulb tip and has a saclike base embedded in a multicellular outgrowth. Whereas the cells the of multicellular outgrowth at the base have a common cellulosic cell wall, the long cell shows high rigidity, and roughness, due to the silica cell wall reinforcement and arrangement, that allows it to work as a tiny needle that deters herbivory.

In response to mechanical injury or high temperatures, or just before dormancy, callose is a polysaccharide that is deposited between the cell wall and plasma membrane. Likewise, callose cell-wall appositions, the papillae, are large physical barriers induced at the sites of pathogen attack (Luna et al. 2011).

Non-glandular or Glandular Structures

Along with the obstacles provided by the chemical compounds mentioned above, that mainly reinforce or seal the cell wall, there are additional plant-environment interaction traits, provided by isolated cells or groups of specialized cells, occurring either internally or externally in the plant body. Moreover the external specialized cells can be either non-glandular or glandular, Fig. 5.1.

Among non-glandular external structures, trichomes (discussed below), thorns (modified branches such as those of *Citrus* spp.), spines (modified leaves such as those of *Ferocactus* spp.), and prickles (slender sharp outgrowths from the cortex and epidermis, such as those of *Rosa* spp.) serve as protective structures providing shade (trichomes), reflecting incident radiation or dissipating heat (trichomes, thorns, spines and prickles) and/or reducing plant herbivory (thorns, spines and prickles). According to Agrawal et al. (2000), spines of *Centaurea solstitialis* (yellow star thistle) may not only deter mammalian herbivory, but also deter lepidoptera which are illegitimate flower visitors. Noteworthy is the special plant-herbivore interaction involving the spines of the bull's-horn acacia (*Acacia cornigera*) and ants (*Pseudomyrmex ferruginea*) that protect acacia from

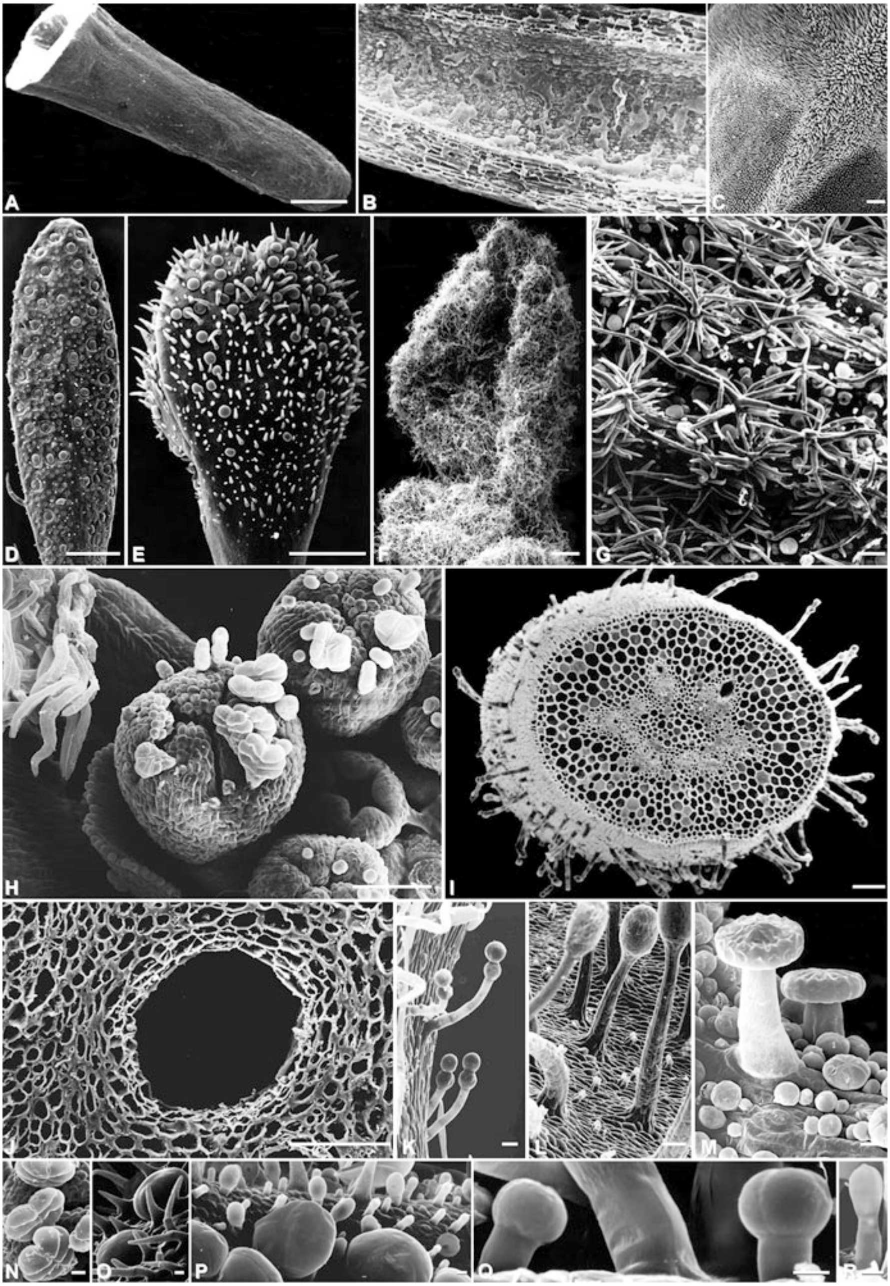

Fig. 5.1 Scanning electron micrographs (SEM) from different types of secretory structures (**a**–**j**) and details of different types of glandular trichomes (**k**–**r**) and non-glandular ones (**o**, **g**). (**a**). Young nectary spur and (**b**). Longitudinal section of the nectary spur of *Limodorum abortivum* (L.) Sw. (Orchidaceae). (**c**). Adaxial glandular epidermis of *Ophrys lutea* (Cav.) (Orchidaceae) labellum. (**D**–**I**). Glandular trichomes on vegetative and reproductive organs. (**d**). Adaxial surface of young leaf and (**e**). Flower bud of *Thymus caespititius* Brot. (Lamiaceae). (**f**). Young leaf and (**g**). Sepal of *Marrubium vulgar*e L. (Lamiaceae). (**h**). Initial stages of development of

herbivores, climbers, and competing vegetation. In return, ants live on the enlarged spine shelters and feed on the extrafloral nectar secreted by foliar nectaries (Heil et al. 2004).

The surface of the aerial parts of plants can also be covered by specialized epidermal cells outgrowths, either glandular or non-glandular trichomes, or other types of secretory cells (nectaries, hydathodes, emergences, osmophores, etc.). This type of external secretory structures are common in plant families such as Araceae, Asteraceae, Cannabaceae, Geraniaceae, Lamiaceae, Orchidaceae, Piperaceae, Plumbaginaceae, Rubiaceae, Rutaceae, Solanaceae, Verbenaceae (Figueiredo et al. 2008a).

Lato senso, trichomes are uni- or multicellular structures that have two types of functions: protective (non-glandular trichomes, or coverage trichomes) or secretory (glandular trichomes) (Tissier 2012). Non-glandular trichomes can form a dense indumentum that prevents water losses, protects against UV radiation and restricts access to insects. The velvety silvery-grey appearance of the surface of many leaf is due to the profusion of this indumentum (*Artemisia* spp., *Helichrysum* spp., *Santolina* spp., etc.). Some species, like common toxic garden plant, oleander (*Nerium oleander*), have stomata sunken in crypts covered with non-glandular trichomes, below the leaf surface. This feature enables reducing the drying effect of warm air and wind.

In some plants, such as the hummingbird plant (*Dicliptera suberecta*), lady's mantle (*Alchemilla vulgaris*), or tomato (*Solanum lycopersicum*) the profusion of non-glandular trichomes exhibits water-repellent properties similar to the Lotus-effect, defined by Hsu et al. (2011) as the Plastron-effect (shield-effect). In lady's mantle, water droplets lay on the trichomes as perfect spheres, without contacting the leaf cuticle, and run off the leaves very easily, without wetting them (Hsu et al. 2011).

The knowledge on both the plant structural features and their popular uses, may also be a source of inspiration for new applications. Based on popular knowledge that strewn kidney beans (*Phaseolus vulgaris*) leaf were used for trapping bed bugs, Szyndler et al. (2013) identified the structural features involved in the mechanical capture by these leaves, in order to design biomimetic surfaces for bed bug

Fig. 5.1 (continued) *Achillea millefolium* L. (Asteraceae) flower heads (Figueiredo and Pais 1994). **I**. Cross-section of *Pittosporum undulatum* Vent. (Pittosporaceae) stem. (**i–j**). Cross-sections of the canals in the (**i**) stem and (**j**) fruit of *Pittosporum undulatum* Vent. (Pittosporaceae). (**k–m**). Glandular trichomes on the leaf of (**k**) *Pittosporum undulatum* Vent. (Pittosporaceae), (**l**) *Drosera capensis* L. (Droseraceae) and (**m**) *Byblis* sp. (Byblidaceae). (**n**). Biseriate trichomes on young florets of *Achillea millefolium* L. (Asteraceae). (**o–p**). Non-glandular trichomes, and peltate and capitate glandular trichomes on the abaxial surface of *Thymus caespititius* Brot. (Lamiaceae) leaf. (**q–r**). Short- and long-stalked capitate trichomes on the abaxial surface of young *Marrubium vulgar*e L. (Lamiaceae) leaf. Bars = 500 μm (**a**, **c–f**); Bars = 100 μm (**b**, **g**, **h–j**, **l**); Bars = 25 μm (**k**, **m**). Bars = 10 μm (**n–r**) (Images reprinted with permission: (**b**). (Figueiredo and Pais 1992), (**h** and **n**). (Figueiredo and Pais 1994). (**f**, **g**, **q** and **r**). (Belhattab et al. 2006). (**i**, **j** and **k**) (Ferreira et al. 2007). (**e**, **o** and **p**). (Figueiredo et al. 2008b) trapping. The capture mechanism involved the physical impaling of bed bug feet (tarsi) by hooked trichomes, in a distinct way from the Velcro-like mechanism of non-piercing entanglement. Using bean leaves as templates, and plant cell walls-like polymers, Szyndler et al. (2013) microfabricated surfaces indistinguishable in geometry from the real leaves, including the trichomes. Despite snagging the bed bugs temporarily they did not hamper their locomotion as effectively as natural bean leaves.

Albeit the enormous diversity of glandular trichomes, in terms of number of cells, size, shape, secretory process, period of secretion and function, they can be divided in two main classes: capitate and peltate trichomes. The complex mixtures of secondary metabolites that accumulate within this structures and their role in plant adaptation are discussed under the chemical features section of this chapter.

Whereas glandular trichomes are examples of external secretory structures, the idioblasts, cavities, canals/ducts, salt glands and laticifers are internal secretory structures common, for instance in Anacardiaceae, Apiaceae, Araceae, Aristolochiaceae, Asteraceae, Calycanthaceae, Fabaceae, Hypericaceae, Lauraceae, Leguminosae, Magnoliaceae, Myoporaceae, Myrtaceae, Pinaceae, Piperaceae, Rutaceae and Saururaceae (Figueiredo et al. 2008a).

From the diversity of internal secretory structures, only one type of idioblast will be mentioned in this structural features section, since the other internal secretory structures accumulate different types of soluble chemical substances, detailed in the next section.

Idioblasts are isolated plant cells specialized in storage of different types of substances. Particularly common is calcium oxalate, which can assume several insoluble forms in the vacuole, depending on the species, the degree of hydration and crystallization conditions. Prismatic crystals are common in the vacuoles from the outer bulb scales of onions (*Allium cepa*); druses, the star-shaped compound crystals, are frequent in oleander (*Nerium oleander*) leaf cells, and on stem cells of hop (*Humulus lupulus*); and the bundles of needle-like crystals, the raphides, occur in banana (*Musa* spp.) pericarp cells, and aloe (*Aloe* spp.) leaf cells. As detailed by Franceschi and Nakata (2005), several studies demonstrated that this biomineralization process functions include, namely, calcium regulation, detoxification (e.g., heavy metals or oxalic acid), ion balance, plant protection and tissue support. Crystal's number, size, shape and placement may discourage herbivory. For example, some studies proposed that extensive crystal formation may provide resistance to bark-boring insects in conifers, and others demonstrated the aversion to oxalate-containing plants by goats. From man point of view, where in abundance, calcium oxalate crystals are released during harvesting and processing of plant tissues, having been correlated with contact dermatitis among field-, flower- and distillery industries workers (references *in* Franceschi and Nakata 2005).

Some plants have evolved specific structural characteristics to face particular stressful abiotic conditions, which are no less important. In conditions of limited water, some plants roll up the leaves, in order to reduce leaf surface and water loss. Other plants evolved taproots that grow deep to reach for water supply. Others accumulate the amino acid proline, or other solutes, creating a water imbalance that allows these plants to extract more water from the soil than other plants. Pneumatophores are special root systems that grow out of water-saturated soils, allowing oxygen to aerate the submerged parts of the root system. The aerenchyma is also a particular leaf parenchyma, developed by aquatic plants, that helps to store oxygen and impairs buoyancy. Pollution, either air pollution (ozone, acid rains, dust), or heavy metals pollution, such as near roadsides, cement factories, tanning industry, mining and quarries works, to name a few, determines gloom, stomata closure and diminishes CO_2 flux (Figueiredo et al. 2008a). Heavy metals tolerant plants tend to be heavy metal type specific, and only few mechanisms of tolerance are well understood. Nevertheless, phytoremediation (bioremediation) of heavy metal polluted soils can be potentially interesting (Sinha et al. 2013). Salty habitats, occurring in deserts, marshes or in seashore line, would cause water lost, wilting and death to the majority of plants, but some became adapted to these environments. These adapted halophytes plants, accumulate sodium and chloride ions in the vacuoles of leaf cells, creating a negative water potential that allows them to take up water more easily. Other halophytes have glandular structures named salt glands. These glands excrete salt that accumulates in the leaf surface and may reduce the loss of water by transpiration. From man point of view, there is a growing interest in not only using some halophytes as a *gourmet* salt substitute to avoid hypertension problems, such as salicornia (*Salicornia* spp.), but also in biosaline agriculture (Lu et al. 2010; Ksouri et al. 2012).

Salt glands, glandular trichomes, as well as other types of external and internal secretory structures, are good examples of combined physical and chemical response by plants. Glandular trichomes, for instance, are by themselves physical barriers, producing a vast array of natural products that the plant uses in its interaction with the environment and man takes profit from them, for instance as essential oils, pharmaceuticals, or ingredients for other applications.

Mimicry and Plant, or Plant Parts, Movements

From the structural point of view there are many other examples whereby plants react to living and non-living factors. Mimicry, although not so much studied in plants, is known for instance in members of the genus *Passiflora* (Passion flowers). Yellow egg-like structures develop in different *Passiflora* plant parts in what is known as *Heliconius* egg mimicry, because *Heliconius* butterflies are dissuaded to oviposit on host plants that possess these egg-like plant structures (Williams and Gilbert 1981; Bhushan 2012).

Also important, and in some cases in the borderline between structural and chemical reactions of plants to environment are plant, or plant parts, movements. Plant movement may occur in response to (a) general factors such as wind, raindrops or passing animals (plants swaying movements), to (b) sun, orienting plant parts either perpendicular or parallel to sun rays, as with sunflowers (*Helianthus annuus*) or cotton (*Gossypium* spp.) and/or to (c) touch as in the sensitive plant (*Mimosa pudica*), or in Venus flytrap (*Dionaea muscipula*). Some of the biochemical processes behind these movements are still not so well understood, but they involve both chemical and physical plant traits. The movement of the bracts in *Dalechampia* species as been interpreted as to avoid nocturnal florivory (Willmer et al. 2009).

2.1.2 Chemical Features

Plants also produce a large variety of organic compounds that help them in their adaptation to abiotic and biotic interactions. These compounds are known as secondary metabolites or natural products, and differ from the primary metabolites, as they have, among others, no direct role in primary metabolism and show a restricted distribution in plants (Figueiredo et al. 2008a). Despite their limited distribution, sometimes limited to a plant species or to a group of plant species, they are chemically very diverse. In a simple way, secondary metabolites can be grouped in terpenes, phenolics and nitrogen-containing compounds which can be characterized by histochemical and analytical procedures. These substances are sometimes stored in the vacuoles in a glycosidic form or accumulated in special secretory structures, Fig. 5.2.

Many MAP accumulate in internal structures, such as idioblasts, cavities, canals/ducts, or in external structures, like trichomes, a blend of monoterpenes, sesquiterpenes, as well as the phenolic phenylpropanoids, and/or sulphur compounds, polyacetyenes, fatty acids, etc., usually extracted from plant material in the form of essential oils, or other complex volatiles extracts. An essential oil is by definition a product obtained by (a) hydro-, steam- or dry-distillation of a plant or of some of its parts, or by (b) a suitable mechanical process without heating, as in the case of *Citrus* fruits (AFNOR 1998; Council of Europe 2010). In this sense, the complex blend of compounds that a plant accumulates in its secretory structures is much more than an essential oil, as the secretion may also contain non-volatile compounds. Nevertheless, for simplicity the terminology adopted will be essential oil. Basil (*Ocimum* spp.), chamomile (*Matricaria* spp.), eucalyptus (*Eucalyptus* spp.), lemon (*Citrus* spp.), peppermint (*Mentha* spp.) or thyme (*Thymus* spp.), are some examples of plants that contain these complex mixtures.

Many essential-oil producing plants were shown to possess a wide range of biological activities. Particularly studied are those properties mostly of man interest, either for health benefit, for agricultural assistance, or for food, and other commodities, preservation purposes (Adorján and Buchbauer 2010). Essentially based on in vitro studies, essential oils and volatile-containing plant extracts have shown several properties such as acaricide and larvicidal (Pohlit et al. 2011), allelopathic (Vokou 2007; Cummings et al. 2012), analgesic and against dementia and Alzheimer's disease (Dobetsberger and Buchbauer 2011), antimicrobial, immuno-modulatory, anti-tumour, anti-apoptotic and anti-angiogenic (Saad et al. 2013), insect repellent (Nerio et al. 2010; Boulogne et al. 2012; Nawrot and Harmatha 2012) and nematotoxic properties (Andrés et al. 2012; Ntalli and Caboni

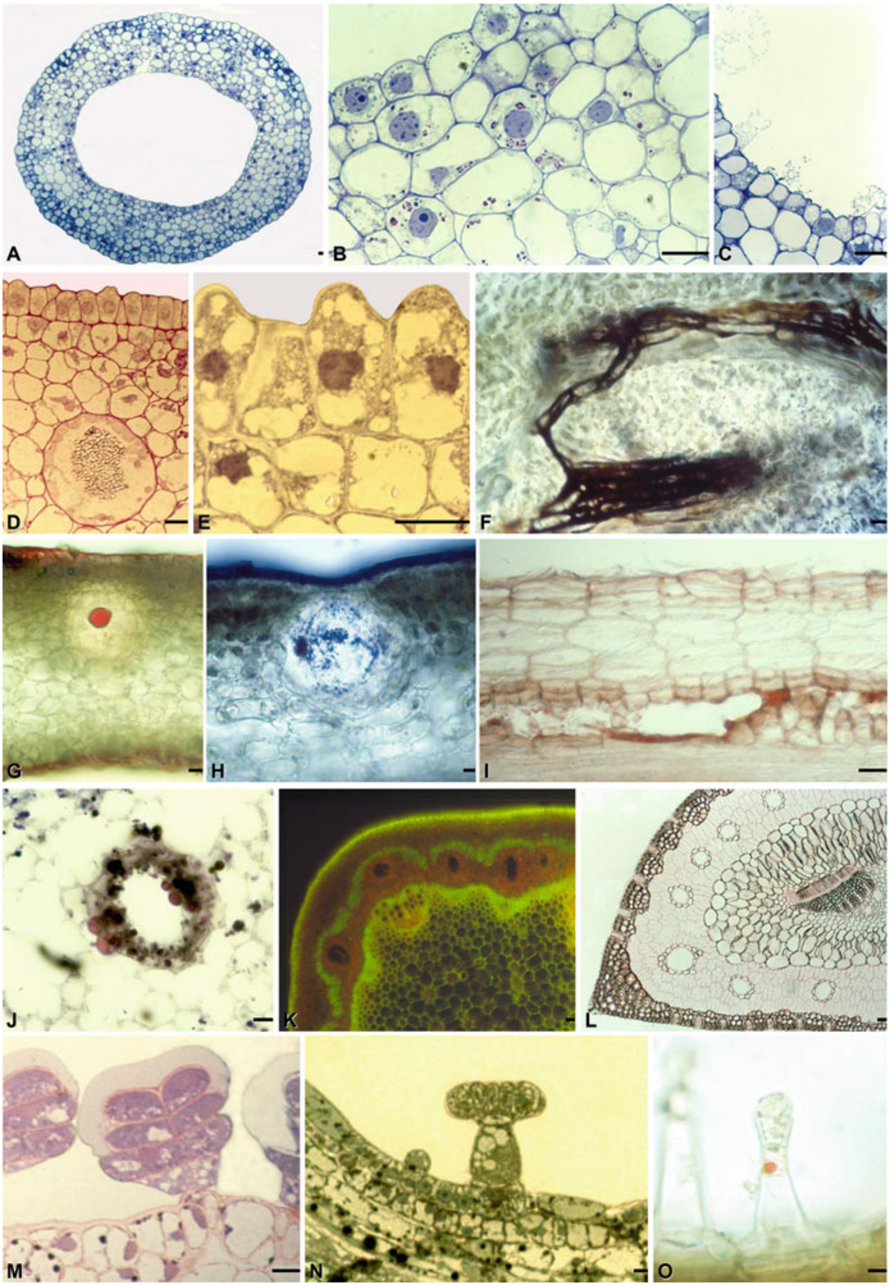

Fig. 5.2 Light microscopy micrographs from different types of secretory structures and histochemical characterization of the natural products present in the secretions (secondary metabolites). (**a**–**c**). Cross section of the nectary spur of *Limodorum abortivum* (L.) Sw. (Orchidaceae). (**d**). Adaxial glandular epidermis of *Ophrys lutea* (Cav.) and of (**e**). *O. fusca* Link (Orchidaceae). (**f**). Lacticifers in the capsules of *Papaver pinnatifidum* Moris (Papaveraceae). (**g**–**h**). Ducts in cross-sections of *Citrus* x *limon* (L.) Burm.f. (Rutaceae) leaf. (**i**–**l**). Canals in (**i**–**j**) longitudinal- and cross-sections of the stem of *Crithmum maritimum* L. (Apiaceae), (**k**) cross-section of

2012; Faria et al. 2013). In addition, essential oils are commercially important for man in flavouring foods and beverages, and making perfumes and cosmetics.

From the plant adaptive interactions point of view, there are an endless number of relations involving chemical communication between plants and other organisms as well as with the environment. Among these the (a) environmental abiotic interactions, (b) the interference in community development, and (c) defence against pathogens and phytophagous, will be highlighted. Indeed, in several cases this separation in different topics results artificial, as in any specific biotic or abiotic system they are all combined. For this reason several examples will fall within more than one topic, i.e., in several cases it is difficult to fix a clear border between the defence against phytophagous, from the interference in community development, as both are interlinked.

Environmental Abiotic Interactions

Albeit the qualitative and quantitative diversity and emission rates, many plant species emit terpenes, from internal or external specialized structures, occurring above (vegetative, flowering and fruit parts) or below ground. Less specialized systems include mesophyll cells occurring in some trees, and examples of more specialized systems are the internal resin ducts in *Pinus*, or the external trichomes of several Lamiaceae or Asteraceae species.

Loreto and Schnitzler (2010) reviewed the influence of abiotic stresses, such as temperature, drought and salt, irradiance, ozone and other oxidants, on the biosynthesis and emission of volatile terpenes. While stressing that the discussion is still enduring they showed examples of the thermoprotective and antioxidant physiological functions of volatile terpenes.

The simplest isoprenoids represent an important class of Volatile Organic Compounds (VOCs) emitted by plants. Not only deciduous trees emit isoprene, but also many plant species emit both isoprene and monoterpenes, such as eucalyptus (*Eucalyptus* spp.), fir (*Abies* spp.), myrtle (*Myrtus* spp.), oak (*Quercus* spp.), spruce (*Picea* spp.) or willow (*Salix* spp.) (Calfapietra et al. 2009).

Abiotic stresses do not only trigger the production of low molecular weight volatile terpenes, such as isoprene, mono- and sesquiterpenes. High-temperature stress induces also the production of heat shock proteins as well as the non-volatile carotenoids and phenolic compounds. Carotenoids are tetraterpenes, that along with

Fig. 5.2 (continued) *Schinus molle* L. (Anacardiaceae) stem and (**l**) cross-section on *Pinus pinaster* Aiton (Pinaceae) needles. (**m–o**). Glandular trichomes on (**m**) *Achillea millefolium* L. (Asteraceae) florets, (**n**) *Byblis* sp. (Byblidaceae) and (**o**) *Origanum vulgare* L. (Lamiaceae) leaf. Fresh material: (**f–k**, **o**). Historesin sections: (**a–e**, **l–n**). Staining and double-staining procedures: Toluidine blue: (**a**, **c**). Toluidine blue-periodic acid–Schiff's: (**b**, **m**). Paragon: (**d**). Alum carmine-green iodine (Mirande reagent): (**l**). Dittmar reagent for alkaloids: (**f**). Sudan III: (**g**, **i**, **o**), and Black Sudan B for lipids: (**n**). Nadi reagent for terpenoids: (**h**, **j**). UV autofluorescence: (**k**). Bars = 50 μm (**a–o**) other terpenes, such as isoprene or α-tocopherol, stabilize and photoprotect the lipidic phase of the thylakoid membranes (Wahid et al. 2007). In fact, carotenoids, and the diterpenes giberellins, or the triterpene derivatives, brassinosteroids, to mention just a few, have so well-characterized functions in plants that they, despite being products from the secondary metabolism, could be considered as primary metabolites.

In addition to their major attraction role, discussed below, flavonoids (anthocyanins, flavones and flavonols) protect the epidermal cells layers of flowers, fruits, leaves and stems from excessive UV-B. Along with their role as UV screen, the accumulation of anthocyanins observed under high temperature stress, seems to be implicated in increased uptake- and reduced water loss by transpiration (Wahid et al. 2007; Miller et al. 2011; Pallozzia et al. 2013).

Interference in Community Development (Allelopathy and Semiochemicals)

Healthy above and below-ground plants parts, as well as decaying plant material, release a huge diversity of secondary metabolites into the environment. The effect of such compounds in nearby community (other plants, microbes and phytophagous) is known as allelopathy. Although allelopathy often applies to the detrimental effects of plants on their neighbours, in a broader sense it includes also the beneficial interactions. Another commonly used term is that of semiochemicals to include the biologically active molecules that function as signalling compounds between organisms. Usually allelochemicals is mostly used for secondary metabolites, whereas semiochemicals include both primary- and secondary metabolites.

From the most common defensive point of view, allelopathy is known for controlling the vegetation composition, their spacing and speed of germination, and interfering in the decay process. If a plant can reduce the growth of neighbouring plants by releasing chemicals into the soil, it will increase its own access to light, water and nutrients, which means having an adaptive advantage. Allelochemicals, and/or semiochemicals, are also an important part of the defensive role against phytophagous.

The importance of allelopathy in natural systems is, very often, questioned, since it is difficult to prove that this phenomenon actually occurs in nature. If it is easy to show, in an *in lab* system, that plant extracts, or isolated compounds, inhibit the growth of other plant species, it is quite difficult to show that they occur in nature, in a concentration high enough to cause the same effect. In the field, the organic substances present in soil can be bound to soil particles, they can remain long or can be quickly degraded by microbes or lixiviated by rain water, both from above or below-ground plant parts. This is however a promising study area by its agricultural, forest and invasive plants management implications (Cummings et al. 2012; Cipollini et al. 2012).

A number of examples exists where microbes interact with plant allelochemicals, either by being their target, by facing community shifts, and/or by either inhibiting or by improving plants allelopathic effects (Cipollini et al. 2012). Some essential oils constituents, namely the monoterpenes camphene, β-myrcene and α-pinene, or sesquiterpenes such as α-longifolene, slow the growth of fungi that otherwise would promote the decomposition of some trees.

In addition to the most common examples of eucalyptus (*Eucalyptus* spp.) (Zhang et al. 2010) or walnut trees (*Juglans* spp.) (Weston and Duke 2003), the sensitivity of several plants to compounds produced by species of *Artemisia*, *Rosmarinus*, *Salvia*, *Sassafras*, *Satureja*, and *Thymus*, to name just a few, is also known. Camphene, camphor, 1,8-cineole, thujones and α- and β-pinene are some of the essential oil components that have marked seed germination and root respiration inhibitory effect, thus interfering with the spacing between plants and with the composition of the community. It is noteworthy that the toxicity of these compounds is quite often enhanced when they are in mixture, comparatively to the isolated compounds. The mechanism behind the synergistic effect is unknown but may involve the ability of a component of the mixture to inhibit the capacity of detoxification mechanisms of the target organism, or to enhance of absorption/penetration of the mixture.

Allelopathic interactions may be very complex, involving very often more than just one emitter and one receiver, as is the case of the tri-trophic system that includes the white-weed (*Ageratum conyzoides*). This weed often invades cultivated fields and is responsible for significant crop losses in several countries. However, according to Kong et al. (2005), intercropping this weed in citrus orchards leads to an effective suppression of other weeds growth and of several fungal pathogens spore germination, and to a population increase of the predatory mite *Amblyseius newsami*, an effective natural enemy of citrus red mite *Panonychus citri*, thus controlling this major citrus arthropod pest at low and non-harmful levels.

Many other examples exist whereby plant released semiochemicals provide some advantage to the plant, but in other cases the biological significance of the released semiochemicals remains elusive. Seeds of parasitic weeds, such as broomrapes (*Orobanche* spp. and *Phelipanche* spp.), and witchweed (*Striga* spp.), can only germinate in response to specific germination stimulants, present in the rhizosphere of both host- and some non-host plants (Zwanenburg and Pospíšil 2013). Almost all germination stimulants are the carotenoid derived terpene lactones, strigolactones. Strigolactones are considered nowadays to constitute a new class of plant hormones that stimulate the germination of parasitic weeds seeds, act also as branching factors for arbuscular mycorrhizal fungi, as well as repressors of lateral root formation and as inhibitors of shoot branching in order to optimize plant growth and development under diverse environmental conditions. Whether strigolactones developed as an adaptation of plants to life on land, by modifying growth and development in response to suboptimal conditions, is still a matter of debate (Brewer et al. 2013).

Interaction with Pathogens and Phytophagous

Virtually all ecosystems have bacteria, viruses, fungi, nematodes, ants, insects and other herbivores (phytophagous organisms in general), responsible for a number of plant diseases, injuries and/or depletion of plants, or plant parts. In all cases, interactions are two-way stories, that is, pathogens and phytophagous attack mechanisms have adapted together with plants defensive mechanisms.

Pathogen mechanisms of penetrating plant parts, either above or below-ground, involve direct access through the surface, wounds or stomata (Zhang et al. 2013). On the other hand, phytophagous can harm the plant in different ways due to diverse feeding habits. Although there are a number of peculiarities in plant-pathogen or plant-phytophagous interactions, it is currently considered that there are also a number of response similarities (Wondafrash et al. 2013; Zhang et al. 2013).

The different forms of cell wall thickening and strengthening, discussed above in reference to the apoplastic barriers, are one first line of pathogen- or phytophagous-induced defence. Because plants have the ability to replace wounded parts by growing new ones, they do no repair damaged tissues. Instead, they seal and induce death of the wounded area cells to restrict the damage. Cellulose, suberin, lignin and callose cell-wall appositions, are some strategies used by plants to intensify the apoplastic barriers and by this way enhancing mechanical and chemical barriers that block plasmodesmata limiting pathogen movement between adjacent cells.

If the pathogens, or phytophagous, are successful in penetrating all the apoplastic barriers, then an immense and complex array of defence mechanisms are triggered, which are discussed in detail by Wondafrash et al. (2013) and Zhang et al. (2013). Receptor-like protein kinases, defensins, phytoalexins, jasmonic acid and ethylene signalling molecules are implicated in nonspecific defence, but they do not all act at the same time, nor at the same speed, and they are not alone in plant response. Plant resistance “immune system” is triggered by membrane-anchored recognition receptors, followed by activation of mitogen activated protein kinases cascade and downstream transcription factors. The resistance genes (R gene)-mediated response to pathogens usually results in hypersensitive response, and activates salicylic acid-dependent signalling, leading to systemic acquired resistance (Wondafrash et al. 2013; Zhang et al. 2013).

As a part of plants defence systems, phytoalexins, low molecular weight antimicrobial compounds synthesized and accumulated by several plant species in response to their exposure to microorganisms, are of utmost importance. Isoflavonoids in Fabaceace (*Medicago* spp.) and sesquiterpenes and polyacetylenic compounds in Solanaceae (*Solanum* spp.) species are just some examples of phytoalexins. The stilbene resveratrol is an example of some plants induced phytoalexin which has gained attention by being connected with health improvement, namely as anti-aging, and having a positive effect on cardiovascular diseases, cancer and atherosclerosis. In addition to being a stress induced metabolite in several plant species, resveratrol is also constitutively accumulated in peanut (*Arachis hypogaea*). Several biotic and abiotic stimuli are being studied to increase its accumulation in peanut with commercial exploitation purposes (Hasan et al. 2013).

Interestingly, grazing is not always considered detrimental (Hegland et al. 2013). Long-term grazing exclusion may have a negative influence on species renewal and productivity (Jing et al. 2013). In many cases plants regrow quickly after grazing, even producing more branched plants than those that are not grazed. Nevertheless, most frequently plant species deter herbivory by using from simple amino acids, such as L-canavanine (Huang et al. 2011), signalling molecules like the systemin peptide (Pearce 2011) or jasmonates, along with many secondary metabolites, namely terpenes, phenolics, glucosinolates or alkaloids.

L-canavanine is a nitrogen storage compound, isolated originally from jack bean (*Canavalia ensiformis*), closely related to the protein amino acid, L-arginine. The toxic effect of L-canavanine to bacteria, fungi, yeast, algae, plants, insects, and mammals is considered to be due to its incorrect incorporation into proteins, in place of L-arginine. Relying on the structural similarity between L-canavanine and L-arginine, and on therefore the competition between these amino acids for various enzymatic reactions, L-canavanine is now being evaluated as a potential anti-cancer drug due to its toxicity to human cancer cells (Huang et al. 2011).

Semiochemicals, such as diverse type of terpenes (cardenolides from *Digitalis* spp., saponins from *Dioscoreae* spp., etc.), phenols (furanocumarins form *Citrus* spp., tannins from *Punica* spp., isoflavonoids from *Trifolium* spp. etc.) and alkaloids (*Lupinus* spp., *Senecio* spp., etc), play also an important defensive role as feeding deterrents. In conifers as, for instance, fir (*Abies* spp.), pine (*Pinus* spp.) or spruce (*Picea* spp.), a constitutive oleoresin comprising monoterpenes, sesquiterpenes, and diterpene resinic acids accumulates in resin ducts, found in the trunk, twigs and needles. These compounds are toxic to several insects, including the world wide conifer species pest, bark beetles. New, induced traumatic resin ducts are observed in the developing secondary xylem (wood) after insect attack, fungal elicitation, and mechanical wounding. In Norway spruce (*Picea abies*), Martin et al. (2002) showed that methyl jasmonate was able to induce these traumatic resin ducts and terpenes accumulation in the developing xylem, a tissue that, in this species, constitutively lacks axial resin ducts.

Some plants developed both structural and chemical strategies to control ant distribution in plant parts, restricting them to foliage rather than to flowers. These tactics involve physical barriers on or around flowers, foliage extrafloral nectaries, which act as chemical lures, and structural barriers located far from the flower, and/or, volatile organic compounds, used as signals to attract ants to leaves and/or deter them from flowers. In some acacia species, repellency involves at least some volatiles that are known components of ant alarm pheromones, and that are not repellent to beneficial bee pollinators (Willmer et al. 2009).

As a part of their defensive traits, plants do not only use direct defense mechanisms, that is, producing compounds that act directly on the phytophagous, but they also use indirect defence mechanisms, which may deter phytophagy and thus increase in reproductive ability (Quintero et al. 2013). This type of defence includes the release of volatile plant signals that attract natural enemies of the phytophagous, such as predators or parasitoids. *Inter alia*, indirect defence and has been reported in cabbage (*Brassica* spp.), cotton (*Gossypium* spp.), cucumber (*Cucumis* spp.), elm (*Ulmus* spp.), Lima bean (*Phaseolus lunatus*), maize (*Zea mays*) and pine (*Pinus* spp.) (van Poecke and Dicke 2004; Degenhardt 2009).

Interestingly, from a man applicability point of view, the knowledge on plant feeding deterrents may be of commercial importance. Actually, in what concerns food selection by insects, feeding deterrents seem to be more important than feeding attractants or stimulants. Thus, grain or seed protection could be achieved by adding some deterrent components to a commodity, as long as the deterrent satisfied a number of conditions, such as (a) absence of toxicity to people, animal and beneficial insects, (b) causing no taste, smell or other commodity characters changes, (c) showing broad inhibition feeding spectrum, (d) showing toxicity at low doses and long-lasting and (e) being stable, easy to apply, leaving no residues, compatible with other products and with low production cost (Nawrot and Harmatha 2012). Despite plants having so many natural defences, many studies, either by conventional breeding or metabolic engineering (Degenhardt 2009; Lange and Ahkami 2013), attempt to provide crop plants with commercial interesting improved traits against herbivores that do not diminish plant fitness.

2.2 Attraction of Pollinators and Seed Dispersers

Apart from the defensive role of plant structural and chemical traits, many of these also act in combination to attract, reward, and sometimes lure, pollinators and seed dispersers.

Each plant must display its best structural and chemical traits to divert the attention of pollinators and seed dispersers from the other plants, to itself. Visual, tactile and olfactory signals are in this sense particularly important to help attracting animals to flowers and fruits. Again it should be stressed that visual, tactile and olfactory features act in combination, probably potentiating each other in pollinators, and some seed dispersers, memory. Moreover, we should look at these interactions on a broader scale, keeping in mind that visual, tactile and olfactory signals will be able to attract both beneficial and opportunistic individuals, that is, the plant is, sometimes, under opposite pressures and a balance must be found between attraction and defence. Indeed, only for simplicity these mechanisms are dealt with separately.

2.2.1 Structural Features

From an adaptative point of view, pollination performed by animals is probably the most important in terms of evolution. Visual and tactile traits involved in plant–pollinator and plant–seed disperser relationships include, in addition to scent (discussed under chemical features), colour, particular structural features of the flower (corolla tubular or pendant, enclosed or open, with or without nectar guide-lines, with or without spurs, with landing platform present or absent, etc.), and a reward which is usually present under the form of nectar and/or pollen. Bees consume both nectar and pollen; birds, butterflies and moths only nectar, and some pollinators are not rewarded at all, but deceived into pollinating a flower, as the example of the spider orchid, discussed below.

Pigments create visual signals and flowers, fruits, as well as other plant parts, use these coloured signals to attract pollinators and seed dispersers. For this reason, colour is more often observed in animal- rather than wind-pollinated plant species. Colour can help animals with plant species selection, flower location and ripeness, and nectar and pollen location within the flower. Petal colours often change over time both associated with flower development and pollination. Thus flowers pigmentation seems to play a major role in pollination process and success. In fruit, colours change as the seeds reach maturity and the fruit ripens, thus ensuring that animals will be attracted to mature fruit and will disperse mature seed (Miller et al. 2011).

Apart from chlorophyll, there are other three main types of pigments which are stored in different plant cells compartments. Carotenoids are terpenoid compounds that accumulate mostly in chromoplasts and are responsible for the yellow, orange and red colours. Flavonoids are phenolic compounds that accumulate in the vacuole. From these, anthocyanins are the most common pigmented flavonoids, responsible for most of the red, pink, purple and blue colours in different plant parts. Anthocyanin colour depends on several factors, such as the degree of hydroxylation and methoxylation groups of the anthocyanin B-ring, the number and type of linked sugars units and on the vacuole pH. Flavones and flavonols are flavonoids that absorb light at shorter wavelengths, invisible to the human eye, but that insects such as bees see as attraction cues. Betalains are nitrogen-containing water-soluble molecules, with restricted distribution, that contribute to red, purple and yellow of some plants.

Bees are able to see in the ultraviolet spectrum and do not perceive the primary colours in the same way as humans do. For instance, if a flower has a corolla with yellow carotenoids at the edge and a yellowish flavonoid in the centre, it will look yellow throughout in visible light. However, for bees, the corolla will be shiny yellow at the edge and with a darker centre. Moreover, many flowers have "honey guides", some only seen in ultraviolet light, that direct the bees to the nectar.

Nature colour palette has become highly important from man point of view, as artificial dyes are being banned from market. Actually, some natural products are able to give colour without interfering with food taste, particularly carotenoids that are being used as natural colouring agents for food, generally for yellow and/or orange colours (Miller et al. 2011). Moreover, the full set of natural colours is also important in nature based colour charts (RSH 2007), which are standard reference for plant colour identification of landscape management, food colourings, fabric designers and chemical engineering.

As stated earlier, particular structural characteristics of the flower are also very important in plant-pollinator interaction. The flower epidermis, for instance, provides visual (discussed above) and tactile clues for pollinators. Floral epidermal surfaces, composed of conical or papillate cells protruding outwards from the plane of tissue, such as in heartsease (*Viola tricolor*), give a more velvety appearance than parallelepiped forms, as is the case in hibiscus (*Hibiscus* spp.), or than common leaf surfaces as in rubber tree (*Ficus elastica*) leaf. Conical petal epidermal cells vary greatly in overall size, and are usually associated with pollination. Whitney et al. (2011) reviewed the effects of conical petal cells on flower form, plant reproductive success and pollinator behaviour. The authors concluded that although the fitness benefits provided to plants were likely to vary with pollinator and habitat, conical petal cells seemed to play a role in enhancing colour by focusing light into petals. Moreover, the cone shape might have a light-scattering effect, generating a sparkling appearance. Also conical epidermal cells provide a grip surface, whereas flat-celled petals are more slippery, showing thus the importance of tactile cues in pollination.

Fruits and seeds have evolved a variety of dispersal adaptations by water, wind or animals. Also in the case of pollen, some flowers have developed amazing close-by structural relationships with certain animals. Stewart (2013), showed that *Orpheum frutescens* is a flower with an exclusive relationship with a particular bee, the carpenter bee (*Xylocopa* spp.). In order to get the pollen from the unusual type of curled stamens, the carpenter bee has to vibrate its wings at a particular frequency, around 261.6 Hz, corresponding to the musical note middle C (or Do in the fixed-Do solfeggio scale). The vibrations make the flower open the stamens, releasing the pollen, covering the bee with the fine yellow powder. This specific relationship ensures that the flowers' pollen is taken only by the carpenter bee to another flower of the same species.

2.2.2 Chemical Features

The capacity of plants to chemically interact with their environment has already ben pointed out with the examples in reference to the defensive role mechanisms. Nevertheless, several of the chemical substances illustrated earlier are also used in attraction purposes. Again these compounds fall down in the classes of terpenes, phenols, nitrogen-bearing compounds and other primary and/or secondary metabolites. However, these substances are often at reduced levels and/or different ratios.

Plant volatile organic compounds play a major role in pollinator's attraction (Farré-Armengol et al. 2013). Not surprisingly then, the volatiles emission is dynamic and very often coordinated with the pollinator activity cycle. The maximum volatiles emission during the night is usually associated with plants with night pollinators, such as bats, mice, or nocturnal moths. In contrast, in plants with diurnal pollinators, the volatiles emission attains its maximum during the day. The honeysuckle (*Lonicera japonica*), was found to synchronize the strongest odour emission with its nocturnal moth pollinator, and the spider orchid (*Ophrys sphegodes*), is a case of highly specialized system with pheromones-like production (references *in* Figueiredo et al. 2008a). This orchid produces the same type of volatile compounds, in similar relative amounts, as those found in the sexual pheromones of the virgin female pollinator cuticle, the bee *Andrena nigroaenea*. Male bees are attracted by the shape and odour of the spider orchid flower, which resembles the virgin female bee. During the so-called pseudocopula with the flower labella, pollinia are transferred to- and carried by the bee. The works of Schiestl et al. (1999, 2000) showed that the odour changes after the pollination is completed, and that farnesyl hexanoate, until then a trace compound, started to increase. This compound is known to inhibit the insect copula when it is present in large amounts on the female cuticle. After the pollination, the combined morphological changes and ending of the volatiles emission, not only saves plant resources but also redirects the pollinators to the still unpollinated spider orchid flowers.

Examples of particular and/or extreme specificity between floral scent and pollinator, can also be found in Canada thistle (*Cirsium arvense*), between figs (*Ficus* spp.) and fig wasp pollinators, or midst yucca (*Yucca* spp.) and yucca moth (*Tegeticula*). Canada thistle floral emissions do not follow ambient temperature fluctuation; it is maximal when pollinators are abundant, and reduced when florivores are active (Theis et al. 2007).

The yucca flowers open at night and attract the yucca moth. Inside the flower the female moth gathers balls of sticky pollen from the stamens of one plant and carries them to another plant. There the moth enters the flowers and pierces the ovary walls, laying eggs in the vicinity of the tiers of ovules. Depending on the species, the moth either packs the pollen balls into the stigma cavities or rubs the pollen across the stigma surfaces, thus effectively pollinating the flowers. As the ovules develop into seeds, the eggs hatch, and the larvae consume some of the seeds for food. When the larvae are fully grown, they bore their way out of the ovaries and after falling into the ground, they burrow into the soil until the next flowering season, when the adults moths emerge. In all but one species, all reproductive behaviours of moths, specifically mating inside flowers, pollination, and oviposition, take place after sunset when yucca flowers are open and fragrant. In the case of *Yucca filamentosa* volatiles, amongst the twenty-one scent compounds, some commonly released by injured plants (*E*-4,8-dimethylnona-1,3,7-triene), as well as characteristic compounds (two di-oxygenated compounds) were found (Svensson et al. 2005). The release of *E*-4,8-dimethylnona-1,3,7-triene in *Y. filamentosa* is apparently not induced by herbivory, because it is emitted constitutively from undamaged floral tissue. According to Svensson et al. (2005), the combination of unique compounds and low variation in the fragrance blend may reflect highly selective attraction of obligate pollinators to flowers.

The stage of development of the plant organ as well as the plant part (leaf, flower, fruit, etc.) can have a major influence in volatiles composition. As detailed in Figueiredo et al. (2008a), volatiles variability can be particularly obvious in entomophilous flowers, since they can act as orientation clues, and thus the flowers volatiles may be distinct from those of the other plant parts.

Pollen and nectar volatiles play also an equally important role in pollinators' attraction, despite their low abundance. Nevertheless, pollen and nectar have nutritional value to pollinators and seed dispersers. Opposite to bees and birds, ants have a limited potential as pollinators (Willmer et al. 2009), anyhow, they are good seed dispersers. The seed appendages from bleeding heart (*Lamprocapnos spectabilis*) or trillium (*Trillium* spp.) contain oils attractive to ants. After transporting the seeds to the nest, the ants remove the appendages for food and do not harm the seeds.

All the plant physiological variability, along with variations imposed by environment make it difficult to have a broad and integrated structural and chemical picture on the plant-animal interaction. In addition, most studies address just one particular topic of the relationship and not all combined. Parachnowitsch et al. (2012) evaluated the scent, floral morphology, corolla colour and life history traits in plants from three populations of the bee-pollinated *Penstemon digitalis*. The emitted scent differed among populations in a common garden, highlighting the possibility of scent being determined by differential selection pressures. Despite the importance of the flower number and display size, selection favoured scent rather than flower size or colour. Linalool was a direct target of selection and its high frequency in floral-scents pinpointed that further studies of both pollinator- and antagonist-mediated selection on this compound are required for understanding scent evolution.

3 Self-Defence in MAP Adaptation

Despite being able to produce a wide range of chemical substances that are toxic to pathogens and phytophagous, plants are able to protect themselves from these toxic chemicals.

In a way similar to that used by some phytophagous that avoid plant toxins, plant self-defence may include modified receptors or modified enzymes, which do not recognize the toxic compound, avoiding its metabolization. This is the case for L-canavanine producing plants, mentioned earlier (Huang et al. 2011).

Another mechanism of self-defence results from the fact that many plants accumulate compounds in a non-toxic form in specialized cells, and the enzymes that convert them into toxic forms in other cells. The active toxic compound is only produced if the plant is, in any way, wounded and the substrate and the enzyme come together. Moreover, only the phytophagous or mechanically damaged plant part will be injured by the toxic compound. This is the case of cyanogenic glycosides in cassava (*Manihot esculenta*), and glucosinolates in broccoli (*Brassica* spp.). Glucosinolates and their hydrolytic enzymes, myrosinases, are good examples of this type of self-defence, as they are stored in separate cell compartments in the intact plant tissue. However, when glucosinolates mix with myrosinases, as consequence of tissue damage, they are rapidly hydrolyzed to toxic isothiocyanates (mustard oils) and other derived products (Winde and Wittstock 2011).

Probably, the most common way of self-defence in plants is to produce and/or accumulate a panoply of toxins, deterrents, repellents either in the vacuole, in the waxes of the cuticle, or in the different glandular structures, such as trichomes, idioblasts, cavities, canals/ducts and laticifers. Some toxic compounds possessing low water solubility/miscibility are glycosylated prior to being translocated to the vacuole. This glycosylation process turns the otherwise toxic compounds into harmless compounds to the cell, by enabling their cellular transport and vacuole storage. Most commonly, the large majority of plant secondary metabolites such as alkaloids, terpenoids and phenolics accumulate in specialized glandular internal or external structures. This segregation process keeps substances away from the chloroplasts, mitochondria and other cellular enzymatic machinery.

4 Conclusion

In addition to the constitutive structural and chemical traits of the plant integrated whole, both structural and chemical characters can be rapidly induced when plant cells detect the presence of any type of biotic and abiotic stresses. Moreover, both constitutive and induced plant structural and chemical characters play a major role in attracting pollinators and seed dispersing animals.

The knowledge on, and understanding of-, these adaptative mechanisms (structure and biological function) can have positive practical implications from man point of view, when using plants in general, and MAP in particular. There are several examples of how man has used plant adaptative traits on his own benefit. Biomimetics, for example, by imitating biology or nature, allows synthesizing products by artificial mechanisms, which mimic the in nature occurring ones. Replication of the so-called Lotus effect has been used to develop a multiplicity of surfaces with superhydrophobicity, self-cleaning, decreased adhesion, and antifouling properties. Any pest, or disease, that is detrimental for plants will be an important threat to food, or other plant derived products production. In this sense, plant pathogen and/or phytophagous resistance is a field to explore by both conventional and genetic engineering plant breeding methods, to create plants with increased resistance, but that concomitantly do not lose plant fitness. On the other hand, the recognition of allelopathic interactions, and/or the response to elicitors, to name just a few examples, can be used in weed and pest integrated management measures in forestry, agriculture, agroforestry as well as in biodiversity conservation.

It should nevertheless be stressed that, when considering management strategies, it is highly important to keep in mind that changes in structural or chemical traits in a plant species may have restraining effects on the interaction with one agent while representing an attraction to other agents. It is thus of extreme importance considering plant interactions as an integrated whole.

Acknowledgments Partially funded by Fundação para a Ciência e a Tecnologia (FCT), under Pest-OE/EQB/LA0023/2011 and UID/AMB/50017/2013.

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