
NECTARIES AND NECTAR

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Cover illustrations from left to right:

Left: Cross section through the base of an ornamental tobacco (*Nicotiana langsdorfii* x *Nicotiana sanderae* Hort var Sutton's Scarlett Line LxS8) flower showing the large, bright-orange floral nectary located at the base of the ovary (picture by Robert Thornburg).

Middle: Flower in an inflorescence of *Fatsia japonica* with large nectar droplets on the surface of the yellow nectary (picture by Massimo Nepi).

Right: *Lycus fernandezii* (Lycidae) drinking nectar of *Aloysia wrightii* (Verbenaceae), New Mexico (picture by Bob Barber).

Background: Scanning electron micrograph of the nectary surface of *Cyclanthera pedata*. Nectar droplets are secreted by multicellular capitate trichomes (picture by Fabrizio Ciampolini).

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Preface

“Nectar is the drink of the gods”... since the time of Homer (the *Iliad*, 800 BC), nectar has been known as a unique biological fluid with mystical properties; yet it is only now that the true chemistry of nectar is being defined. Nectar is a complex biochemical milieu offering much more than sugars to visiting pollinators. Its consumption is central to one of two types of plant–animal interaction that have contributed so much to global biodiversity: herbivory and pollination. All types of plants, regardless of their position on the evolutionary scale, are eaten by herbivorous animals. Nectar, however, is the product of a mutualism in which animals consume nectar and are involuntarily responsible for the transport of pollen or, in some cases, for plant defence. The presence of nectaries, in either reproductive or vegetative parts of a plant, symbolizes that plant’s benevolent relationship with animals.

Nectaries are interesting not only for our knowledge of plant biology, but also because they are involved in the pollination of many edible and rare plants, thus having huge economic and ecological importance. About a third of our food may be derived from bee-pollinated crops. In addition, nectar is the raw material of honey. Other than bees, nectar is food for an enormous variety of insects, a tenth of all bird species, and some mammals; when nectar is not an animal’s main food, it often provides an energy drink. Nectar biology has many overlapping facets, evident in the chapters that follow: botany, chemistry, zoology, and ecology.

The stimulus for this volume was the meeting of a group of nectar biologists in Italy, at the first international conference dedicated exclusively to nectar and nectaries. The meeting was held in Montalcino, Tuscany, in May

2002, and the proceedings were published as a special volume of *Plant Systematics and Evolution* (238, issues 1–4, 2003). The topics ranged from the molecular biology of tobacco nectar to the potential effects of global climate change on floral nectar production, and we decided it was the right time for a new book on nectar. The cooperation of the three co-editors was also assisted by an award from the Joint Italy/South Africa Science and Technology Agreement (2002–2003).

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Chapter 1

INTRODUCTION

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1 EVOLUTIONARY ORIGINS

The evolutionary origins of nectaries and nectar are relatively obscure, but several researchers, working on a broad scale on the evolution of angiosperm families, have provided overviews of nectary incidence, diversity, origin, and function. Two contrasting examples below show how concepts regarding the origin of nectaries and nectar have been modified in the light of new information. Firstly, in his outline of the classification of the angiosperms, Armen Takhtajan (1980) gives a simple, concise statement on the purpose and origin of nectaries:

The original pollinators were most probably beetles The original attractant in insect pollination was the pollen But the necessity for pollen economy leads to a course of evolution in which the flower starts producing a cheaper foodstuff, nectar, as its alternative. For the production of nectar special structures are formed as nectaries. They originated independently in the most diverse lines of angiosperm evolution and on a most widely varying morphological basis. With the emergence of nectaries the plant gets an opportunity for producing pollen in more limited quantities and using it only for transport to other flowers.

Later, based on new data from paleobotany and molecular systematics, Peter Endress (1994a) discusses recent concepts of the evolution of angiosperm flowers and states:

The reward(s) to pollinating insects in early angiosperm flower evolution were floral secretions, and not pollen, in contrast to earlier hypotheses. The pollination drop on the ovular micropyle and later the stigmatic secretion may have served as nectar reward for pollinators...

The first two lines of Tahktajan's statement were disputed in the light of new evidence from different sources, but Endress also presents the concept that nectaries may have multiple evolutionary origins and can be induced in a wide range of positions and tissues in the flower (Simpson & Neff, 1983).

The history of ideas about nectaries and nectar shows that it was a long time before the role of nectar in insect pollination was recognized: earlier it was assumed that nectaries originated as excretory organs to rid the flower of superfluous liquid (Lorch, 1978). This physiological explanation for nectar-secreting structures was recently revived by de la Barrera and Nobel (2004), in the context of the carbon and water relations of flowers. According to their "leaky phloem" hypothesis, nectar secretion could result from high hydrostatic pressure in the phloem and the structural weakness of developing phloem tissue. Their complementary "sugar excretion" hypothesis is based on sugar accumulation due to rapid growth and associated high transpiration rates of floral structures. However, we consider the primary function of nectaries to be ecological rather than physiological, as sites where liquid substances involved in interactions with animals are produced and offered in exchange for benefits to the plant. Animals that are attracted by nectar rewards not only involuntarily disperse pollen in the environment, thus enabling plants to avoid self-fertilization and competition with parents and siblings, but may also help protect plants from herbivores.

The most ancient extant plant with nectaries is the bracken fern *Pteridium aquilinum*, which has extrafloral nectaries on its fronds (Heads and Lawton, 1985). The phylogeny of extant seed plants shows three separate origins of animal pollination: in cycads, gnetaleans, and angiosperms (Pellmyr, 2002). In gymnosperms, secretions resembling nectar occur in Gnetales and are involved in pollination (Bino et al., 1984; Wetschnig & Depisch, 1999). Nectaries are far more common in angiosperms, dating back to the late Cretaceous. Early-branching lineages of the angiosperms (the ANITA grade, based on molecular studies) are characterized by tiny flowers with wet stigmas, the stigmatic secretions being a potential reward, included among plesiomorphic traits in angiosperms (Endress, 1994a, 2001). Most angiosperms are pollinated by insects, which are rewarded with nectar during visits to flowers with floral nectaries, whereas extrafloral nectaries reward a more limited set of animals, mainly ants, that keep herbivores away.

Nectaries are specialized tissues that secrete a sugary solution involved in interactions with animals. The term does not indicate a uniform or well-defined anatomical structure, however (Fahn, 1979; Pacini et al., 2003). There are various types of nectary, situated anywhere in the flower and in widely different parts of plants, with different origins and types of organization. The diversity of nectaries is evident in Vogel's exhaustive description of the types and structures of nectaries in many angiosperm families (Vogel, 1997, 1998a,b,c). In general terms, nectaries consist of three components (Fahn, 2000; Pacini et al., 2003):

- An epidermis, with or without stomata and trichomes, where nectar is released to the exterior.
- Specialized parenchyma that produces or stores nectar solutes.
- The vascular bundle that conveys water and nutrients to the parenchyma.

The conventional view that nectar originates from phloem sap but may be modified by the nectary parenchyma is perhaps oversimplified. The sugar component of nectar is derived from photosynthesis by the nectary itself, or probably more commonly by photosynthesis in other parts of the plant, with or without starch as an intermediary storage product. At least some extrafloral nectaries, which secrete for prolonged periods, photosynthesize. The breakdown of stored starch makes high rates of nectar production possible, at any time of the day (Pacini et al., 2003).

2 SECRETIONS ANALOGOUS TO NECTAR

The floral secretions mentioned by Endress (1994a) as potential early rewards to pollinating insects were pollination drops and stigmatic secretions. The exposed ovules of gymnosperms secrete a sugary fluid at the micropylar end, and this so-called pollination drop acts as a nectar reward for insects in *Gnetum*, *Ephedra*, and *Welwitschia* (Owens et al., 1998; Gelbart & von Aderkas, 2002). Strong evolutionary, cytological, and chemical similarities exist between the pollination drop and nectar. Both are liquids containing carbohydrates and proteins. The function of the pollination drop is to rehydrate pollen and to serve as germination medium, and rehydration of pollen grains is only possible if the sugar concentration of the drop is relatively low: more concentrated solutions would tend to dehydrate it. Retraction of the pollination drop draws pollen into the ovule, whereas nectar is consumed by animals visiting the flower and may be reabsorbed if not collected by visitors. Pollination drops always retract to draw pollen into the micropyle, whereas reabsorption of unconsumed nectar only occurs in some species,

mainly those investing heavily in nectar production and having many ovules per ovary, such as *Cucurbita pepo*, *Linaria vulgaris*, and certain orchids (Pacini et al., 2003).

The stigma of many plant species exudes liquids consisting mainly of lipids that facilitate pollen adhesion, but in some monocots (e.g., certain Araceae) the stigmatic secretion is a clear sugary fluid containing few or no lipids (Heslop-Harrison & Shivanna, 1977). The watery exudate forming drops on the spadix of *Anthurium hookerianum* contains 7% sugar (Vogel, 1983). In *Asclepias syriaca* the exudate produced by the stigmatic chamber moves through a capillary system to nectar reservoirs, which are visited by insects. The nectar thus functions as both germination medium for pollen and reward for pollinators. Its concentration may increase through evaporation, but rates of pollen germination are highest in sucrose solutions of 11–15% w/w (Kevan et al., 1989). This shows a clear link between the functions of stigmatic secretions and nectar.

In the vegetative and reproductive organs of angiosperms there are other types of cells and tissues secreting liquids with different ecological functions, not always related to plant reproduction and dispersal. Analogies between nectary and other secreting tissues are more evident when the secretion is liquid and “exported” outside the organ. In certain flowers elaiophores may produce a reward rich in lipids (Vogel, 1988), and osmophores produce a fragrance attractive to animals (Effmert et al., 2005). Vegetative parts, mainly leaves, of plants living in wet environments may have hydathodes, structures that passively secrete water and excess mineral ions from xylem vessels by a process known as guttation (Feild et al., 2005). According to Feild et al. (2005), this process may be defensive in that it prevents flooding of the mesophyll. Carnivorous plants have modified leaves covered with various glands which function in attracting and digesting the prey (Joel, 1986). Pitcher plants (*Sarracenia* and *Nepenthes*) have large extrafloral nectaries above the pitcher (Dress et al., 1997; Owen & Lennon, 1999). All these types of secretory cells have been considered and analysed from an anatomical point of view (reviewed by Fahn, 2000). The structural similarity between nectaries, hydathodes, and elaiophores has often been noted (Schmid, 1988; Vogel, 1997).

Sugary secretions are also produced by fungi and insects. Fungal infection of the ovary of *Secale cereale* (Poaceae) attacked by *Claviceps purpurea* (Ascomycetes) elicits production of a sugary fluid that the parasite exploits to disperse its conidia (Alexopoulos et al., 1996). The comparison with nectaries is valid from an ecological point of view, because the pathogenically induced

exudate attracts insects that disperse the spores. The cost of fungal spore dispersal is, however, at the expense of the reproductive function of the plant. Wäckers (2002) gives other examples, such as rust fungi that produce, near their spores, sugar droplets consumed by dispersing insects.

Honeydew is the greatest non-floral source of sugar, and was probably a flight fuel for insects before the appearance of flowering plants. It is the excretory product of homopteran insects, such as aphids, whiteflies and scale insects, which must feed more or less continuously on phloem sap in order to obtain sufficient nitrogen. The excess sugar and water in their diet is excreted as honeydew, which differs from nectar in containing oligosaccharides synthesized by the insects from the dietary sugars. The sugar composition of honeydew depends on both the sap-sucking homopteran and its host plant and, in addition to sugars, amino acids from the phloem are also excreted to some extent (Byrne & Miller, 1990; Völkl et al., 1999). It was suggested by Downes and Dahlem (1987) that honeydew use may have preceded nectar feeding in early Diptera, which appeared long before the angiosperms: the pseudotracheate labellum of flies would have been ideal for dissolving and then imbibing dried films of honeydew on leaves. These sponging mouthparts are likewise suited for drinking stigmatic secretions which, like honeydew, are shiny fluids which would be visually attractive to flies. The fossil history of surface fluid feeding involves a wide range of imbibed fluids, not necessarily involved in pollination (Labandeira, 2002).

Many small insects such as flies, ants, and parasitoid wasps meet their carbohydrate requirements from a mixture of floral nectar, extrafloral nectar, and homopteran honeydew, although in laboratory experiments it has been found that the oligosaccharides in honeydew are less likely to elicit feeding responses and are of less value nutritionally (Wäckers, 2000, 2001). Ants in Australian rainforests obtain sugar and amino acids from many different nectar and honeydew sources (Blüthgen et al., 2004). Ants frequently tend phloem-feeding homopterans, protecting them from natural enemies in exchange for carbohydrate-rich fluids (Völkl et al., 1999). Honeydew is also a valuable sugar source for honeybees, particularly in forests when nectar is in short supply, and honeydew and other sugary fluids may substitute for nectar in the diets of nectarivorous birds (Paton, 1980; Gaze & Clout, 1983). Finally, the manna mentioned in the Biblical chapter Exodus was apparently honeydew produced by a scale insect (*Trabutina mannipara*) associated with tamarisk; it accumulates when attending ants are absent (Bodenheimer, 1947; Ben-Dov, 1988).

3 FLORAL AND EXTRAFLORAL NECTARIES

Two types of nectaries, floral and extrafloral, were recognized by Bonnier (1879). They may differ considerably in anatomical structure, source of nectar components, and mode of presentation (Davis et al., 1988; Pacini et al., 2003). Nevertheless, both have the same function: to reward animals that provide the mobility which plants lack—vectors for pollen dispersal and ants for physical defence—and their exudates are chemically similar. Floral nectaries, however, are better known than extrafloral ones and receive more attention in this volume. The reason for this “asymmetrical knowledge” is that floral structure and the different reproductive strategies of plants have long intrigued biologists and have resulted in comparatively more attention being directed to floral nectaries. These nectaries are also important sources of food for honeybees and are involved in the reproduction of many plants of economic significance and in the production of many fruit and seed crops. Extrafloral nectaries, which occur mainly in tropical plants, are noteworthy from an ecological point of view, but have limited economic applications, at least at present. Some of the differences between floral and extrafloral nectaries are summarized in Table 1. Koptur (1992) provides a detailed review of the interactions between insects and plants mediated by extrafloral nectaries.

Extrafloral and floral nectaries may be found in the same plant species with their secretion being collected by different kinds of animals. The structure, composition, and ecology of extrafloral and floral nectaries in the same species have been compared in various papers, e.g., *Croton sarcopetalus*, Euphorbiaceae (Freitas et al., 2001); *Tabebuia serratifolia*, Bignoniaceae (Thomas & Dave, 1992); *Thryptomene calycina*, Myrtaceae (Beardsell et al., 1989); *Turnera ulmifolia*, Passifloraceae (Elias et al., 1975).

The distinction between floral and extrafloral is topographical, but this separation is artificial. The distinction is certainly not clear in the genus *Euphorbia*, where the extrafloral cyathial nectaries are very close to the flower and are involved in pollination even if this is not clearly stated in the literature (Proctor et al., 1996, Fig. 2.16). Floral nectaries of *Ruellia radicans* (Acanthaceae) produce dilute nectar collected by hummingbirds. The nectary does not cease its secretory activity after the corolla has fallen, but continues producing nectar with a higher sugar concentration, collected by ants (Gracie, 1991). This example is important because it demonstrates that nectary cells may produce nectar with different concentrations according to developmental stage and ecological necessities. The higher concentration of nectar

Table 1. Summary of the main differences between floral and extrafloral nectaries.

	Floral nectaries	Extrafloral nectaries
Function	Reward animals transporting pollen	Reward animals defending plant from herbivores
Position	In different parts of flower: ovary, stamen, calyx, corolla, receptacle	Common in leaves: petiole, stipule, blade Less often in developing inflorescence, e.g., <i>Euphorbia</i> , on floral parts (e.g., calyx or corolla) and developing or mature fruit, e.g., certain Bignoniaceae (Thomas & Dave, 1992)
Nectar consumers	Insects: especially Hymenoptera, Diptera, Lepidoptera Birds: e.g., hummingbirds, sunbirds Mammals: e.g., bats, small marsupials	Mainly ants
Duration of secretion	Few hours to several days, rarely exceeding a week as in <i>Helleborus</i> (Vesprini et al., 1999)	Few days in “tender” young growth, few weeks (when in fruit) to months (nectaries last as long as leaves)
Amount of nectar produced	Less than 1 μ l to few ml: proportional to the nectary parenchyma volume	Generally few μ l per day
Variability of nectar quality	Chemical and physical features (viscosity) vary widely in relation to different nectar consumers	Nectar physicochemical features vary less because ants are main consumers

during the extrafloral phase may be related to greater exposure of these photosynthesizing nectaries to light once the corolla falls.

Benefits to plants from the associations between ants and extrafloral nectaries are not always obvious. Extrafloral nectaries of ferns are best studied in the cosmopolitan bracken *P. aquilinum*, and are hypothesized to provide rewards for ants that defend the plants from herbivores. Experiments with British populations of bracken have, however, seldom provided any evidence that ants visiting foliar nectaries influence levels of herbivory (Heads and Lawton, 1985; Heads, 1986). In South African populations these extrafloral nectaries confer protection only when ant densities are high and homopterans

producing honeydew are also present (Rashbrook et al., 1992). In these experiments the ants strongly preferred honeydew to foliar nectar.

4 NECTAR COMPONENTS

Nectar composition varies widely, quantitatively more than qualitatively, presumably because it is produced to reward different kinds of animals (Faegri & van der Pijl, 1979; Cruden et al., 1983). Not surprisingly, nectar consumers and pollen vectors are primarily taxa that have evolved the ability to fly—insects, birds, and bats (Pellmyr, 2002). However, nectar rewards also attract many non-pollinators. Dissolved substances in nectar have multiple functions: in addition to rewarding animals with water, ions, carbohydrates, amino acids and low molecular weight proteins, nectar contains scented compounds to attract consumers (Raguso, 2004), and enzymes and antioxidants to maintain homeostasis of nectar composition (Carter & Thornburg, 2004). It may also contain toxic compounds to discourage unwanted consumers (Adler, 2000). For solutes other than sugars and amino acids, there is generally much more information available for floral nectars than for extrafloral nectars. Although many constituents of nectar originate in phloem sap, the latter fluid is more difficult to sample than nectar and studies comparing the composition of both fluids in the same plant are rare (for studies comparing phloem sap and extrafloral nectar see Baker et al., 1978 for *Ricinus communis*; Pate et al., 1985 for *Vigna unguiculata*).

The major constituents of nectar (see Nicolson & Thornburg, 2007, Chapter 5 in this volume) are given below, with a brief indication of their origins and their importance for animal consumers. Only for the carbohydrate component of nectar are the origins well understood. The early emphasis was on the energetics of the relationship between flower and pollinator, based on considering nectar as predominantly a sugar solution and also on the high energy demands of many pollinators. More attention is now being paid to the non-sugar components of nectar (it was Herbert and Irene Baker who first drew attention to these; Kevan, 2003) and to their role in pollinator attraction and nutrition. This is by no means an exhaustive list: see Jakubská et al. (2005) for an example of the chemical complexity that becomes evident when nectar is subjected to suitable analytical techniques.

Water. Depending on nectary structure, water may be derived from both xylem and phloem or phloem alone, with a lower water content being expected as the proportion of phloem in the vasculature increases. Nectar water content depends on floral microclimate, and may be greatly affected by

evaporation in exposed flowers. The nectar concentration determines its viscosity and hence influences the feeding responses of animals; water in nectar may also be an important reward for pollinators in dry conditions.

Carbohydrates. The main nectar solutes are the sugars sucrose, glucose and fructose, and their total concentration ranges from 7% to 70% w/w. Invertase activity in the nectary determines the proportion of sucrose to hexoses. Considerable attention has been paid to the question of whether the relative proportions of these three sugars in nectars are a result of adaptation to pollinators (Baker & Baker, 1983; 1990) or phylogenetic history (e.g., Nicolson & van Wyk, 1998; Galetto & Bernardello, 2003). Other monosaccharides and disaccharides may be present in minor amounts, as well as oligosaccharides such as stachyose, and sugar alcohols such as sorbitol. However, oligosaccharides are much less abundant in nectar than in honeydew. Sometimes polysaccharides may be responsible for a jelly-like consistency of nectar (Sazima et al., 2001). The sources of nectar carbohydrates are phloem sap (in which case nectary parenchyma is reduced or absent); photosynthesizing nectary parenchyma, starch stored in parenchyma and derived from photosynthesis in that tissue or other floral parts, or the degeneration of certain nectary parts (Pacini et al., 2003). Sugars in nectar are usually the primary energy source for consumers, and the study of plant–pollinator relationships has long been based on energetics, with clear correlations between the sugar content of flowers and the energy requirements of the animals pollinating them (Heinrich, 1975).

Amino acids and proteins. Amino acids are the most abundant nectar solutes after sugars, and include a wide array of both essential and non-essential amino acids, as well as some non-protein amino acids (e.g., Petanidou et al., 2006). Proteins occurring in nectar include enzymes and preservatives (Carter & Thornburg, 2004). These nitrogenous components are derived from one or more of the following sources: phloem sap, protein bodies in the nectary parenchyma, cytological activity or degeneration of certain parts of the nectary, or the epidermis of the nectary parenchyma. Nectar amino acids may play a role in taste preferences of insects (Gardener & Gillman, 2002) and in their nutrition, depending on other food sources (Mevi-Schütz & Erhardt, 2005). Proteins appear to have various homeostatic and regulatory roles.

Ions. These are derived from xylem and/or phloem sap, although information on ion concentrations in floral nectars is scarce. Again, the nutritional benefits to pollinators will depend on other food sources. High K^+

concentrations in the nectar of onion flowers have a deterrent effect on honeybees (Waller et al., 1972).

Antioxidants such as ascorbate are involved in nectar homeostasis (Carter & Thornburg, 2004).

Lipids are a high energy source but usually occur only in trace amounts in nectar. In some flowers, oils secreted by elaiophores or glandular trichomes are offered as rewards instead of nectar.

Terpenoids. Volatile terpenoids are important components of floral scents (Raguso, 2004) and may accumulate in nectar.

Secondary compounds associated with resistance to herbivory have often been documented in floral nectar (Adler, 2000). Toxic compounds such as phenols and alkaloids may have a selective effect on pollinators, deterring some and attracting others.

Cytoplasmic remnants result mainly from holocrine secretion where the secretory cells break down in the process, e.g., *Strelitzia reginae* (Kronstedt-Robards et al., 1989), *Glycine max* (Horner et al., 2003).

Spores of fungi and bacteria dispersed in the air may fall into nectar, especially if it is exposed, and grow. Thus nectar may be a portal for plant pathogen infections. However, antimicrobial substances with a homeostatic function may prevent the spread of harmful organisms (reviewed by Carter & Thornburg, 2004), because examples of infection are rare. In only a few cases have these invasions been demonstrated to occur via the nectar. Spores of the mould *Aureobasidium pullulans* and *Cladosporium herbarum* enter the nectary via the nectar and destroy extrafloral nectaries in the leaves of *Ailanthus altissima* (Clair-Maczulajtys & Bory, 1982). The pathogen bacterium *Erwinia amylovora*, the agent of fire blight also enters flowers via nectar (Bubán et al., 2003).

Nectar should be seen as a complex and dynamic fluid. Pollinators reduce the volume, sometimes stimulating further secretion in the process, and contaminate it with microbes. Changes in nectar sugar are caused by activity of the nectary (secretion or reabsorption) as well as removal by foragers, which may stimulate further secretion. Nectar water content depends on activity of the nectary, removal by foragers, and is additionally affected by equilibration with ambient humidity (Corbet, 2003). This is particularly noticeable in the more exposed extrafloral nectaries. The resulting spatial and temporal variation is a frequent theme in subsequent chapters.

5 ORGANIZATION OF THIS VOLUME

Two major volumes on nectar and nectary biology were published in 1983 and are long out of print: *The biology of nectaries* (Bentley & Elias, 1983) and *Handbook of experimental pollination biology* (Jones & Little, 1983). The publication of *Nectary biology* (Bahadur, 1998) was delayed and the volume is not widely available. Endress' (1994b) book, *Diversity and evolutionary biology of tropical flowers*, first considers the nectary per se, from a morphological point of view, and subsequently from a systematic point of view in families where it is present. It also provides some historical background to the study of flowers and nectaries. *The natural history of pollination* by Proctor et al. (1996) is an update of an earlier edition and a detailed account of pollination biology. The publication of three books dealing with the practical aspects of pollination biology (Dafni, 1992; Dafni et al., 2005; Kearns & Inouye, 1993) indicates strong interest in this field in recent years. The topical theme of specialization versus generalization in pollination systems has led to a new multi-author volume (Waser & Ollerton, 2006). Volume 238 (2003) of *Plant Systematics and Evolution*, entitled *Nectary and nectar: from biology to biotechnology* and edited by A.R. Davis, M. Hesse, M. Nepi and E. Pacini, is devoted to papers presented at a meeting held in Montalcino in Tuscany, Italy, in 2002. In the journal *Ecology* 2004, vol. 85 there is a special section devoted to papers on *Community and Evolutionary Ecology of Nectar*, with contributions on both floral and extrafloral nectaries from different ecological points of view.

The present book, *Nectaries and nectar*, emphasizes both the plant side of the interaction (nectary structure and function) and the animal viewpoint (nectar composition and consumption). The remaining seven chapters are organized into four conceptual areas, which are discussed in more detail below.

Nectary systematics (Chapter 2)

This chapter reviews the distribution of floral nectaries throughout the angiosperms in a systematic context. Nectar-secreting tissues show great variety in their location and histological structure, previously surveyed in dicots and monocots respectively by Smets (1986) and Smets et al. (2000). Plant diversity is often linked to adaptive radiation of pollination systems, and the variety of nectar-secreting tissues is to some extent associated with the varying morphology and behaviour of pollinators. However, there is also a strong relationship with specific plant phylogenetic lineages, and hence to plant

systematics. In some plant families the nectaries differ greatly in position, morphology, and nectar composition, while others are relatively homogeneous. Species of either small or large families may resemble each other in nectary organization but others, such as Ranunculaceae, show wide variation.

Nectary structure and nectar production (Chapters 3 and 4)

Nectary structure may vary with nectary position in the flower. Though nectary histological components have long been recognized, ultrastructural studies of secretory cells are revealing new details of organelles during nectary development and secretion. Independently from the anatomical organization, the extent of nectary parenchyma determines the quantity of nectar produced and hence the type of pollinator. The anatomical diversity of nectaries may be matched by a similar diversity in the mechanisms of nectar secretion and presentation. The concept of secondary nectar presentation, namely when nectar is not exposed close to the nectary but elsewhere in the flower, as in spurs, was recently developed.

Nectar components may be produced and elaborated in different parts of the nectary tissue. It is generally assumed that nectar carbohydrates are derived from phloem sap, but photosynthesis in the nectary parenchyma may be an important supplementary source of carbohydrates. The storage of starch in non-photosynthesizing nectaries is an advantage when rapid production of nectar is required. We discuss the dynamics of nectar production, including reabsorption of unconsumed nectar. The interaction between the dynamics of nectar production by the plants and nectar feeders defines the nectar standing crop. Animal–plant interactions also affect the site and manner of nectar presentation. Variability in nectar quantity and quality is apparent at many different spatial and temporal levels and is strongly affected by environmental parameters.

Nectar chemistry and molecular biology (Chapters 5 and 6)

The chemical complexity of nectar has been apparent since the prolific work of Herbert and Irene Baker, but analytical methods have naturally improved and a new look at nectar chemistry is appropriate. Nectar sugar composition has been extensively studied, particularly the relative proportions of sucrose, glucose and fructose, and the data have pointed to convergence in nectar characteristics of unrelated plant species and pollinator type (Baker & Baker, 1983); however, the fact that there are phylogenetic constraints on the adaptation of nectar to pollinators has become more apparent in recent years. Nectar is also much more than a dilute sugar solution, and there is renewed

interest in its non-sugar components, such as proteins which inhibit microbial growth, amino acids which contribute to taste and the nitrogen balance of pollinators, and alkaloids and phenols which deter certain pollinators but not others. The water component in nectar, greatly affected by microclimatic conditions, is an important factor in pollinator drinking rates and water balance.

The molecular biology of nectar is a relatively new area of research. Chapter 6 describes the developmental processes that change the *Nicotiana* floral nectary from a non-secretory organ into a secretory one. There is a dramatic decline in levels of starch in the nectary to produce sugar for nectar production. A general analysis of gene expression in nectaries is included, with special reference to proteins with a defence function against microbial attack.

Nectar consumption and ecology (Chapters 7 and 8)

Flowers differ in size by orders of magnitude, and so do their nectaries and the volumes of nectar produced for nectar-consuming animals, which range from 10 mg flies to 30 g bats. Nectar, especially in more open and accessible flowers, is also consumed by nectar robbers, which provide no benefit to the plant. The most numerous nectar consumers are found in three of the four largest insect orders (Diptera, Lepidoptera, and Hymenoptera), and nectarivorous birds and bats provide reliable pollination services in warmer parts of the world. Nectar feeding has physiological implications for all these animals in terms of water, energy, and nitrogen balance, but many are able to utilize nectars of varying composition and concentration. As stressed by Galetto and Bernardello (2003), “success in attracting pollinators is a relative matter”, depending on alternative nectar sources available, so animal visitors should not be too particular. The ability of flower-visiting animals to deal with all kinds of nectar seems appropriate in view of the broad generalization apparent in many plant–pollinator relationships.

Most of the individual studies on nectaries, nectar, and nectar consumers included in this book concern a few plant species (either sympatric or related) and a few animal species that visit them. The final chapter takes a much broader approach, examining nectar resources at the community level in Mediterranean habitats. The information is derived from a unique data set including extensive analyses of nectar sugars and amino acids, combined with a complete survey of insect visitors. It has enabled consideration of several hypotheses about the evolutionary ecology of nectar production in Mediterranean environments, where summer drought is common, flowers

tend to produce small volumes of concentrated nectar, and bees are the dominant pollinators. The role of pollination mutualisms in structuring communities is a rich and rewarding field of study.

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