

Progress in Botany

Ulrich Lüttge
Wolfram Beyschlag
John Cushman *Editors*

Progress in Botany 75

 Springer

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Volume 75

Series Editors

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ISSN 0340-4773

ISBN 978-3-642-38796-8

ISBN 978-3-642-38797-5 (eBook)

DOI 10.1007/978-3-642-38797-5

Springer Heidelberg New York Dordrecht London

Library of Congress Control Number: 2013950980

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Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

Series Information

Progress in Botany is devoted to all the colourful aspects of plant biology. The annual volumes consist of invited reviews spanning the fields of molecular genetics, cell biology, physiology, comparative morphology, systematics, ecology, biotechnology and vegetation science, and combine the depth of the frontiers of research with considerable breadth of view. Thus, they establish unique links in a world of increasing specialization. All chapters are thoroughly peer-reviewed by at least two independent referees.

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Part I

Review

Ants, Plants and Fungi: A View on Some Patterns of Interaction and Diversity

Andreas Bresinsky

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Abstract Biodiversity is a challenging field of research. Approaches are manifold and mostly cover few aspects of the total wealth of phenomena only. The mapping of the vascular plants and the inventory of Basidiomycota in Bavaria are projects to be mentioned in this context as one part of the commitment of the author. In the following article the author describes further activities during his lifework in regard

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to ant–plant interactions resulting in dispersal and distribution of plants, and moreover, in respect to speciation and to evolution of high ranked taxa within the fungi, discussed mainly in relation to the genus *Pleurotus* and the order Boletales. In fungi the investigations include breeding systems, isolation barriers, polyploidy, pigment patterns and DNA phylogeny. The pigment patterning in Boletales correlates well with the phylogeny as revealed by DNA analysis of selected gene sections.

1 Introduction

It is a great honour for me to be invited by the editor of this book series, “Progress in Botany”, to discuss the results of studies which came about following my scientific interests in the review of my life. My doctoral thesis on the dispersal of seeds and fruits by ants had been published 50 years ago (Bresinsky 1963). Taking that study as a kind of my personal starting point, I intend to focus on rather different scientific topics on which my research work was directed. An arch has to be spanned in order to link such different organisms as ants, plants and fungi. Ecological interactions between these groups of organisms would basically allow to develop a consistent presentation. However, actually it is impossible for me to report on my work without taking into account some frictions in the context. Looking back on my life as a scientist, dealing mostly with plants and fungi, I regret that my work had not been concentrated in a more stringent manner on a single integrative topic including all of the mentioned organismic groups.

Being able to perform my life in the world of science came true by the guidance and efforts of my deceased teachers: Dr. Hans Doppelbaur and Fritz Beinroth in the period when I was going to school in Augsburg, and the professors Karl Mägdefrau, Hermann Merxmüller and Josef Poelt in the time when I was visiting the University at Munich. I am grateful that an enriching personal friendship from which I draw permanent benefit until now developed to all of them over the time. After my graduation from the Ludwig-Maximilians-University in Munich I started with my professional career as an employee of well-known institutions, first at the Technical University (TH under Prof. Dr. O. Kandler) and then at the Bavarian State Collection of Botany (Botanische Staatssammlung under Prof. Dr. H. Merxmüller), both in Munich. A really lucky turn in my life was my appointment as full professor and head of a research unit (Lehrstuhl) at the newly established University of Regensburg where I spent the greatest part of my professional life. A highlight during this time in Regensburg certainly was the delegation to the task of convening the International Mycological Congress which had been attended by 1,600 participants from 60 different nations (Hawksworth 1991).

2 Seed Dispersal by Ants

The tremendous biodiversity on the globe has to be studied in respect to historical–phylogenetical developments (evolution) on one side, and in respect to ecological adaptations on the other side. Both modes of interpretation in regard to biodiversity have their own justification and their own importance. A debate about the status and the dominant role of either one of both approaches makes no sense.

2.1 *The Challenge of Biodiversity*

In more recent studies on biodiversity it is the integration of both approaches allowing to achieve a consistent view. I was much impressed by the field trips offered more than 60 years ago by my academic teacher Karl Mägdefrau, because he introduced the students to the diversity of plants not simply by telling their names and their position within the classification but rather by discussing different groups of plants according to their ecological interrelationships. That was quite appealing in respect to a didactic and scientific approach as well. The way Karl Mägdefrau dealt with the ecological background of biodiversity was not an experimental one, it was not one to measure and analyse environmental parameters, but it was much more directed by the interpretation of features of external and internal structure in respect to the challenge to which plants are confronted with in their different environments. In this sense he was obviously not a representative of an analytically and experimentally based ecology which had become more and more important since a while. His attitude to deal with ecology in a mostly non-experimental mode was clearly connected with his main scientific interest in plant life of the earlier geological periods. In this area of research he was well known in his time, and it is obvious that, in this case, he could achieve approaches in the ecological understanding of biodiversity only through interpretation of correlative interrelationships between structures and environmental conditions as far as these are explorable at present. His standard work on the palaeobiology of plants (Mägdefrau 1935; Paläobiologie der Pflanzen 1. ed.) offers a number of examples for such a kind of approach. It might have guided him in choosing topics to be investigated in doctoral theses.

2.2 *Scientific Approach to Myrmecochory*

Thanks to the suggestion of Karl Mägdefrau the task had been given to me to deal with an interesting subject which is still in the focus of recent research (Mayer et al. 2005; Peternelli et al. 2008; Pfeiffer et al. 2010; Fokuhl 2008; Fokuhl et al. 2007, 2012; Boiero et al. 2012): studies on the phenomenon of ant-mediated dispersal of

seeds and fruits with special regard to elaiosomes. My decision to deal with this subject had been debated somewhat critically within the then existing community of supervising and learning persons at the Institute of Botany (“Nymphenburg”) of the University in Munich. You got to hear controversial statements as for instance “senseless study of more or less meaningless structures (i.e. the elaiosomes causing the spreading of seeds by ants) without ecological importance for dispersal”. From today’s viewpoint I have to appreciate the critical discussion of those days because the communicated arguments prevented me to be fixed to a given attitude towards the subject I had to investigate.

Actually, many of the diverse interactions between ants and plants give us the impression of mutualistic interrelationships. One example of these interactions is the uptake, transport and dispersal of seeds and fruits if they are equipped with nutrient-rich appendages, the so-called elaiosomes (Fig. 1). Classical investigations on this topic have been accomplished by Sernander (1906). Rutger Sernander (1866–1944) was able to demonstrate that elaiosome-equipped dispersal units (diaspores) are regularly dispersed by ants. In the course of the diaspore-directed activity of ants, it is only the elaiosome which will be damaged or eaten while the seeds or fruits remain intact. As a matter of fact, the publication of Sernander first dealing with this phenomenon has to be dated back some years earlier when he was coining the broader designed term synzoochory (Sernander 1901) which includes among others the dispersal of diaspores by ants. He made lipids (oil), which are regularly present in the elaiosomes, responsible for the transportation of diaspores by ants. According to Sernander diaspores with detached elaiosomes are mostly less attractive for ants; it was also him (Sernander 1927, according to Wagenitz 2003) who created the term diaspore comprising all kinds of dispersal units of plants regardless their structure and developmental origin (homology). Moreover, he described the basic features of a syndrome characteristic for plants dispersing their diaspores by the aid of ants. In regard to its critical and careful attitude the monograph of Sernander (1906) has to be seen as a distinguished example of a study on a special mode of dispersal (of plants by ants; myrmecochory). Within the history of botany by Mägdefrau (1992) the study has found an honourable position in the chapter “plants in their environment”.

Worldwide there are more than 3,000 species of herbs, shrubs and trees with diaspores being equipped with structures to ensure dispersal by the aid of ants (Beattie and Hughes 2002). In a more recent survey the number of myrmecochorous species worldwide is roughly estimated to be 11,000 in 334 genera and 77 families (Lengyel et al. 2010). In Central Europe the share of plants out of the total number of species (in Angiosperms, seed plants) being equipped with structures for ant dispersal is comparatively low. However, if the share is related to special units of vegetation or to some of the phenological periods then it might be quite considerable (Ellenberg 1996, for plant species of beech forests flowering in spring time). In the frondose woods (Querco-Fagetea excl. Prunetalia and Alno-Ulmion) of Bavaria the share of myrmecochorous representatives out of all 341 species is 14.8 % and even increases to 18.4 % in the herbaceous and grass layer (Bäumler 1984). In the summergreen deciduous forests of Europe and in those of Northeast America

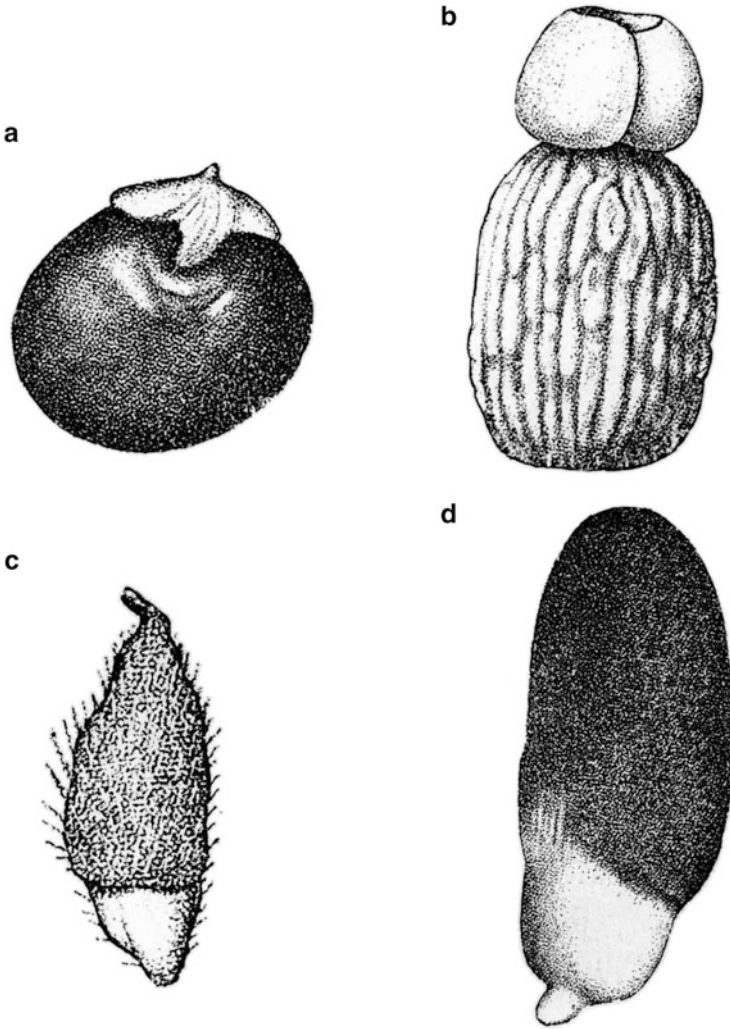


Fig. 1 Diaspores (seeds **a–b** or fruits **c–d**) with attached elaiosomes. (**a**) *Moehringia trinervia* (see also Fig. 2a). (**b**) *Euphorbia myrsinites* (see also Fig. 2b). (**c**) *Hepatica nobilis* (see also Fig. 2c). (**d**) *Melampyrum cristatum* (see also Fig. 2e). After Sernander 1906 in Morton 1912 (Fig. c), Morton 1912 (Fig. a, b, d)

myrmecochory (up to 30 % of the species flowering in spring; Lanza et al. 1992) is mainly restricted on the ground vegetation (Sernander 1906; Kusmenoglu et al. 1989). Myrmecochory was also found to be a device of dispersal in the shrubland vegetation of South Africa (in 20 % of the species) and of Australia (Bond and Slingsby 1983; Berg 1975). Elaiosomes are adapted to the prevailing environmental conditions. The elaiosomes from plants of temperate woods are soft and usually decay in a rather short time if not eaten by ants whereas those from arid areas are

tough, resistant and may persist for a longer time (Beattie 1985). Only few reports are published on myrmecochory in the tropics. There, different from the temperate regions, myrmecochory is often bound to the life form of trees (phanerophytes). In a tropical research area 21 different species of ants in nine different genera ranging in size from 0.1 to 1.2 cm were observed to interact with elaiosome-equipped seeds (Horvitz and Beattie 1980). Also leaf-cutting ants like *Atta sexdens rubropilosa* are active in seed dispersal there (for instance in case of the plant species *Mabea*; Peternelli et al. 2008).

2.3 *Ontogeny, Anatomy and Histochemistry of Elaiosomes*

At the time when I began my investigations, the anatomy and histochemistry of the appendages on seeds and fruits (diaspores) mediating myrmecochory were only insufficiently explored. The reason for it was the fact that the required sections through the hard outer layers of the diaspores on one side and through the adherent soft appendages with big and thin-walled cells on the other side were not easily to be accomplished. Using a special cutting technique (freezing microtome, embedding of the material to be cut in frozen gelatine) it was possible to obtain reasonable sections (Fig. 2). The development (ontogeny) of the elaiosomes was investigated by using regular microtome techniques. The formation of elaiosomes as myrmeco-attractive structures from quite different parts of seeds, fruits and even inflorescences (as it is also realised in case of the devices to ensure dispersal by wind, anemochory) clearly favours the idea of a strong selective pressure behind it in order to ensure dispersal (Bresinsky 1963). However, at the same time there is also a selective pressure effective to avoid damages to diaspores caused by ants. Taking this into account then the myrmeco-attractive appendages on diaspores could even be interpreted as devices to distract ants from the essential parts of diaspores in regard to their reproductive function. This argument is weakened by the fact that diaspores with removed elaiosomes are mostly unattractive for ants.

Myrmeco-attractive appendages on seeds can arise from the outermost layers of the exterior integument (the so-called sarcotesta of *Puschkinia*, *Ornithogalum*). In case of *Puschkinia* the myrmeco-attractive cells of the integument have the shape of concave watch glasses. Their longitudinal extension is ten times that of the cells in the layer underneath. At the end of their hypertrophic development the cell walls are Sudan positive indicating the presence of a triglyceride. A more advanced localisation and morphology of elaiosomes on seeds is accomplished in different ways: through reorganisation of the outer integument beneath the micropylar region in case of *Scilla*, *Chionodoxa*, *Euphorbia* and *Polygala*, of the chalaza region (opposite to the micropyle) in case of *Galanthus* and *Luzula*, of the raphe (which is a strand of a vascular bundle adnate to anatropous ovules) in case of *Helleborus*, *Asarum*, *Chelidonium*, *Stylophora*, *Corydalis*, *Reseda* and *Viola* pr. p., of the funiculus (a caudicle-like structure bearing the ovule) in case of *Moehringia*, *Claytonia*, *Primula* and *Sarothamnus*. The histological rearrangements in the

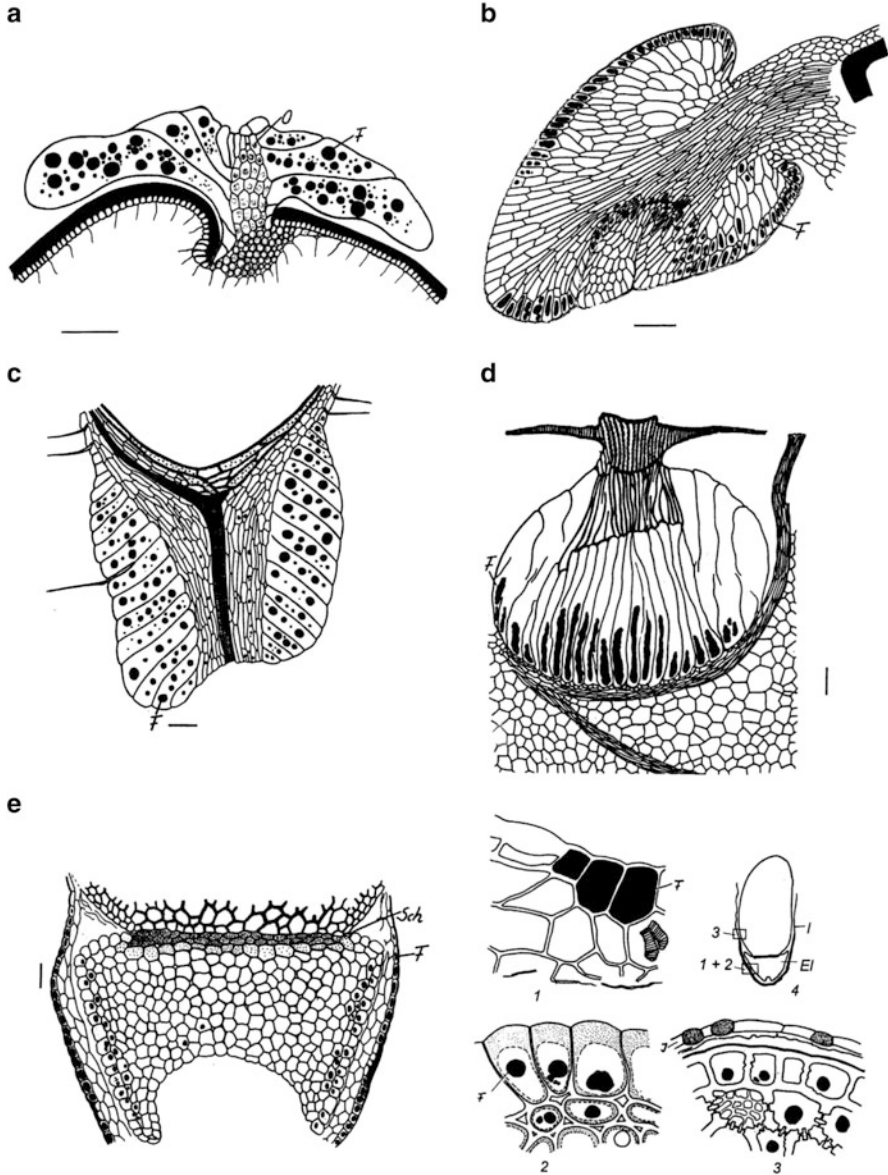


Fig. 2 Anatomical structures of elaiosomes and of adjacent tissues at the diaspores. F = oil (fat), O = oxalate crystal. Bar equals 100 μ m. (a) *Moehringia trinervia*. (b) *Euphorbia amygdaloides*. (c) *Hepatica nobilis*. (d) *Pulmonaria* spec., top diaspore with elaiosome, below fruit axis with vascular bundle serving as abscission layer. (e) *Melampyrum pratense*. *Left side*: The endosperm is divided into an upper part for the nutrition of the embryo and into a lower part with the function of an elaiosome, between both parts an abscission layer (Sch) with introusception of tannins (black). The outer loose envelope is formed by the integument. *Right side*: (1) outer cells of the integument, (2) outer cells of the elaiosome, (3) outer cells of seed above the abscission layer and (4) seed with elaiosome (EI) and integument (I). (1) + (2) and (3) = location of the thin sections in the diagrams (1)–(3) (Bresinsky 1963)

mentioned parts of the ovules mostly include a higher rate of cell division, hypertrophic growth of cells and accumulation of special compounds (lipids, etc.).

A special mode of forming the elaiosome could for the first time be described in case of *Melampyrum* (Figs. 1 and 2; Bresinsky 1963). It throws a particular light on the functional interpretation of elaiosomes. Performing no other important function, it is simply unthinkable that a part of the nutritional tissue of the seed (the endosperm) is detached and thus being lost as nutritional potential for supporting the embryo; hereby the primary function of the endosperm (nutrition of the embryo) is considerably reduced. The endosperm of seed plants arises in the course of a double fertilisation. So it becomes a triploid tissue in two different steps, first through fusion of two nuclei in the primordial ovule and then through fertilisation of the diploid nucleus with a haploid nucleus from the pollen tube. In case of *Melampyrum* about one-third of the total endosperm is pinched off and separated from the remaining endosperm by an abscission layer, in a way that damage to the endosperm serving for the nutrition of the embryo is avoided. The separation into two different functional parts would not make sense in regard to dispersal, if the endosperm were covered and protected by a firm seed coat. In *Melampyrum* such a seed coat does not exist, because the integument from which a seed coat regularly arises is only developed to a thin and loose membrane partly enveloping the seed and which may be easily removed from the seed. It is also the integument cap that stores lipids in its outer cells (Fig. 2e). This integument cap is composed of three cell layers in the area of the elaiosome. It becomes much thinner towards the part where the embryo is embedded or even is missing on the top of the seed. The decisive parts of the seed (i.e. the embryo and its surrounding endosperm) are not protected by an integument-borne seed coat but rather by thick-walled cells in the outer layer of the endosperm and further through a tannin-containing abscission layer between the elaiosome and the rest of the seed. In contrast to the main part of the seed serving the nutrition of the embryo the outer cells of the elaiosome are thin-walled and include myrmeco-attractive oil. The findings support the idea that all these structures depend on a selective pressure favouring the dispersal of the seeds by ants and protecting at the same time the embryo and its nutritional tissue. The mimicry theory (ants take and carry the seeds of *Melampyrum* because of some kind of imitation of their larvae or pupae) will be discussed later.

Finally the cases of elaiosome bearing fruits have to be mentioned. In these cases elaiosomes are formed from the exocarp (*Ballota*, *Lamium*, *Anemone*, *Hepatica*, *Ranunculus ficaria*, *Adonis*, *Fedia*), from the receptacle (*Symphytum*, *Pulmonaria*, *Rosmarinus*, *Ajuga*), from the axis bearing the developing fruit (*Aremonia*, *Potentilla* Sect. *Fragariastrum*, *Thesium*), from the persistent basal part of the style (*Carduus nutans*), from the perianth or perigone (*Parietaria*, *Danthonia decumbens*, *Knautia*, *Centaurea* pr. p., e.g. *Centaurea montana*), or from parts of the inflorescence with several reduced flowers, e.g. from reduced parts of spikelets of grasses (*Melica* pr. p., e.g. *M. nutans* with four reduced flowers integrated in the elaiosome; *M. uniflora*).

The assignment of elaiosome development to a special primordial part of seeds and fruits is sometimes not distinctly feasible because the origin may be somewhat

ambiguous. Different parts of the ovule contribute e.g. to the elaiosome of *Viola* (the raphe and the funiculus). The origin may also be uncertain or only deducible from general viewpoints of development, e.g. in case of *Centaurea* pr. p. or *Knautia*: it might be debated whether the elaiosome develops from the envelope or from the axis of the flower. Because of the same reasons of ambiguity the typification of myrmecochory by Sernander (1906), based on function and morphology, has some weak points.

In floral biology the term syndrome is used for the consonance of several features directed to special pollinators. Also in case of myrmecochory it is possible to sum up several properties as a syndrome favouring or enabling the dispersal of diaspores. These are morphological and chemical features. Morphologically the myrmecochory syndrome is characterised by often colourless, juicy-soft, frequently rather voluminous appendages (elaiosomes) as a part of the diaspores. The cells of the elaiosomes are often hypertrophic (Fig. 2a) and contain lipids and other ant-attractive compounds. Sometimes the lipids are stored in the exterior cell walls or cells of the elaiosomes (Fig. 2b, d, e). Quite commonly special feeding barriers against entry into the essential parts of diaspores are established between the elaiosome and the seed or fruit, like tannin-containing cells (Fig. 2e), thick-walled cells or oxalate crystals (Fig. 2a). The exposition of diaspores close to the ground is also a part of the myrmecochory syndrome in temperate frondose woods (Sernander 1906). Not all of the above-mentioned features have to be present simultaneously in order to ensure myrmecochorous dispersal. However, in Central Europe the combination of many or even all of these features are linked with myrmecochory.

In the Mediterranean in evergreen frondose woods and in shrub communities or in Atlantic heath lands some shrub species with a dissemination of diaspores comparatively high above ground (*Rosmarinus*, *Sarothamnus*, *Ulex*) are myrmecochorous, where at first the diaspores may be set free by a ballistic mechanism. Also in Central Europe not all of the myrmecochorous plant species expose their diaspores directly on the ground. Quite a number of species disperse their diaspores by means of a ballistic mechanism or some other device in a wider area around the mother plant, and are then carried off by ants (dichory: some species of *Viola* pr. p., *Euphorbia*, *Lamium*, etc.). Some plants realise a combination of wind dispersal (anemochory) and myrmecochory whereby, however, those structures enabling wind dispersal seem to be reduced (*Centaurea cyanus*) or less effective (*Melica nutans*). A combination of endozoochory and myrmecochorous synzoochory is given in the grass species *Danthonia decumbens*: the plant gets dispersed when the diaspores are passing the digestive tract of cattle (endozoochory) or if they are picked up by ants (synzoochory) because of the myrmeco-attractive tissue on the palea at the ripening stage of flowers (Sernander 1906).

2.4 *Myrmeco-Attractive Compounds in Elaiosomes*

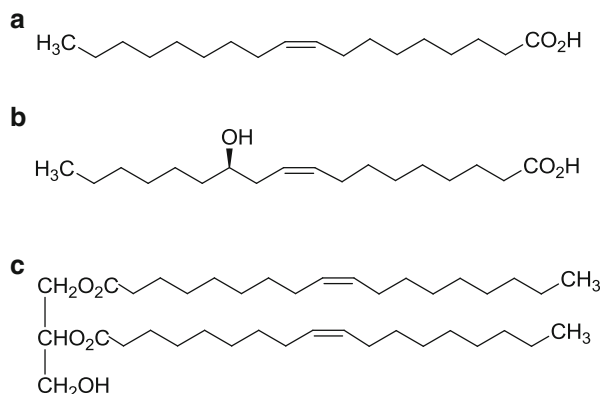
Orientation in the environment and social behaviour of ants are regulated by chemical signals (Wilson 1965; Hölldobler 1978; Bradshaw and Howse 1984; Morgan 2008). In regard to the chemical basis of myrmecochory one has to distinguish between stimulants, attractants and nutrients. The orientation of ants in their environment can be optionally olfactory or gustatory. The stimulants, including those emitted from elaiosomes, are perceived by antennation and answered by some kind of a special reaction. The mode of perception is regarded to be mainly gustatory through direct contact of the antennae with the source of stimulation and less important, if at all, by olfaction of volatile compounds via the air in some distance from the elaiosome (Sheridan et al. 1996). The ants are not attracted by visual cues (Bond and Slingsby 1983; Gammans et al. 2006). The myrmeco-attractive compounds regularly occurring in elaiosomes are lipids (Sernander 1906; Bresinsky 1963) and sugars (Bresinsky 1963). These compounds can be interpreted as attractants and at the same time as nutrients. Moreover, compounds like proteins and vitamins have been detected in elaiosomes (Bresinsky 1963); however, because of sporadic occurrence their function may be not so decisive as compared to lipids and sugars.

2.4.1 Lipids

Lipids are stored in elaiosomes in the form of triglycerides (Sernander 1906; Bresinsky 1963; Kusmenoglu et al. 1989; Lanza et al. 1992; Boulay et al. 2006), diglycerides (Marshall et al. 1979; Skidmore and Heithaus 1988; Kusmenoglu et al. 1989; Lanza et al. 1992; Boulay et al. 2006; Peternelli et al. 2008) and as free fatty acids (Bresinsky 1963; Skidmore and Heithaus 1988; Lanza et al. 1992; Gammans et al. 2005; Boulay et al. 2006; Fischer et al. 2008; Peternelli et al. 2008; Boieiro et al. 2012).

The histochemical proof of triglycerides was done by staining with Sudan III (Sernander 1906; Bresinsky 1963). The use of Sudan III has the advantage that the localisation of the lipids can be microscopically specified in the cells of a tissue and the disadvantage of some degree of non-specificity (e.g. also waxes eventually react). In the case of a missing reaction with Sudan III the lipids may be present in form of diglycerides or as free fatty acids. Actually a proof of the occurrence of a free fatty acid (identified as ricinoleic acid; Fig. 3) could be provided in elaiosomes which did not show any reaction with Sudan III (Bresinsky 1963). In more recent studies advanced separation techniques for identification of lipids have been applied such as thin layer chromatography, column chromatography (Marshall et al. 1979) and gas chromatography (Bresinsky 1963). Using the latter method it became possible to increase considerably the number of free fatty acids being detected in elaiosomes (Skidmore and Heithaus 1988; Peternelli et al. 2008; Pfeiffer et al. 2010). However, the presence of the unsaturated hydroxy fatty acid, ricinoleic

Fig. 3 Chemical structures of oleic acid (a), ricinoleic acid (b), 1,2-diolein (c)



acid (Fig. 3b) in elaiosomes, (Bresinsky 1963) could not be verified by subsequent studies (Marshall et al. 1979; Kusmenoglu et al. 1989; Peternelli et al. 2008).

Regarding their controversial results the findings mentioned above have to be discussed in some detail (Marshall et al. 1979 versus Bresinsky 1963). In subsequent investigations since 1963 it could be demonstrated that diglycerides with unsaturated oleic acid as component (1,2-diolein; Fig. 3c) are important in relation to myrmecochory. According to these investigations diolein is widely distributed in elaiosomes and in higher quantities than other types of lipids. It stimulates certain species of ants (*Aphaenogaster* spec.) to pick up and transport diaspores with elaiosomes (Marshall et al. 1979). The results have been confirmed in some subsequent studies. On the other side it became apparent that in some of the myrmecochorous plants in North America (*Sanguinaria canadensis*, *Trillium sessile*, *Dicentra cucullaria*) the quantities of diglycerides were inconspicuous as compared to the content of triglycerides. Out of four investigated species only in one of them (*Jeffersonia diphylla*) the quantity was high enough for detection of 1,2-diolein in their elaiosomes (Kusmenoglu et al. 1989). In some subsequent studies it was reported that the elicitors for uptake and transport of diaspores through ants are obviously not the diglycerides but rather free fatty acids, especially oleic acid (Boulay et al. 2006; Pfeiffer et al. 2010). Further, one has to consider that triglycerides and diglycerides presumably split off fatty acids; this might happen regularly in the presence of lipases.

In my own investigations a simple method which was available at that time (1960) had been used for the separation of fatty acids following Nowotny et al. (1958) (chromatography on petroleum impregnated paper with the solvent glacial acetic:water 8:1). Applying this method the saturated fatty acids remained at or near the starting point. Also the triply unsaturated linolenic acid was not migrating at a considerable longer distance, whereas ricinoleic acid followed close to the front line and turned black if treated with vapours of osmic acid (OsO₄: an unspecific reaction with the double bonds in alkyl-chains). Using such a rather crude procedure of separation also other hydroxylipids would show similar behaviour as ricinoleic acid. Therefore this kind of proof was taken as ambiguous and

preliminary (Bresinsky 1963; see p. 27 and Fig. 79) in regard to the elaiosomes of *Melampyrum*, *Melica*, *Luzula*, *Veronica* and *Viola* as well as for the larvae of a species of ants.

In order to verify the then assumed occurrence of ricinoleic acid in elaiosomes gas chromatography was applied taking the elaiosomes of *Melica nutans* for investigation. The experiment was performed by A. Prox at the Institute of Organic Chemistry at the Technical University in Munich. Lipids were extracted from the elaiosomes of *Melica nutans* and the free fatty acids were methylated. The run of the extracted and methylated fraction of lipids demonstrated the occurrence of free ricinoleic acid without doubt. Additionally the ant's response to ricinoleic acid was tested in a laboratory nest with the species *Lasius fuliginosus*. Small squares of filter paper soaked with a solution of ricinoleic acid (0.01 %) and also test objects with some other fatty acids (incorporated in the same manner on squares of filter paper) were exposed in an area outside the centre of the nest. Paper squares with ricinoleic acid found vivid interest by the ants and were picked up and transported at a higher rate than paper squares soaked with oleic acid or linolenic acid or the control (bar squares of filter paper; Fig. 4). However, squares cut from the chromatogram in the area of ricinoleic acid were ignored, presumably because it was not possible to remove all of the solvent and of the petroleum impregnation from the chromatogram paper.

Ricinoleic acid is to be distinguished from oleic acid by the presence of a hydroxygroup at C-12 (compare Fig. 3a, b); otherwise the structure of both fatty acids, each with a double bond at C-9, is identical. Even in the investigation of Marshall et al. (1979) it became evident that most of the antennation reactions of *Aphaenogaster* spec. came about in relation to test objects with ricinoleic acid; however, transport of test objects was observed only if they were treated with 1,2-diolein. Several saturated fatty acids (with a shorter carbon chain than ricinoleic or oleic acid) serve the function of trail pheromones in *Lasius fuliginosus*, indicating that chemoreception in this species is largely based on a variety of different fatty acids (Huwyler et al. 1975). Nine saturated or non-saturated fatty acids with a longer chain (e.g. C₁₄, C₁₆, C₁₈, C_{18:1}, C_{18:2}, C_{20:4}) than in the case mentioned above are the components of the trail pheromone of the ant species *Pristomyrmex pungens* (Hayashi and Komae 1977); the identified C_{18:1} fatty acid is similar to or identical with oleic acid.

Without restricting the validity of the results of Marshall et al. (1979), it has to be stated that comparability of results depends on using the same species (of ants and plants) under standardised conditions of the test procedure. Moreover, subsequent studies of several investigators have shown that it were not in all cases diglycerides with oleic acid as component, even not always free oleic acid, which released transport activity of the ants (Lanza et al. 1992; Gammans et al. 2006). Further it was shown that the lipid composition in elaiosomes may depend on the time of seed ripening and on the degree of maturity (Peternelli et al. 2008).

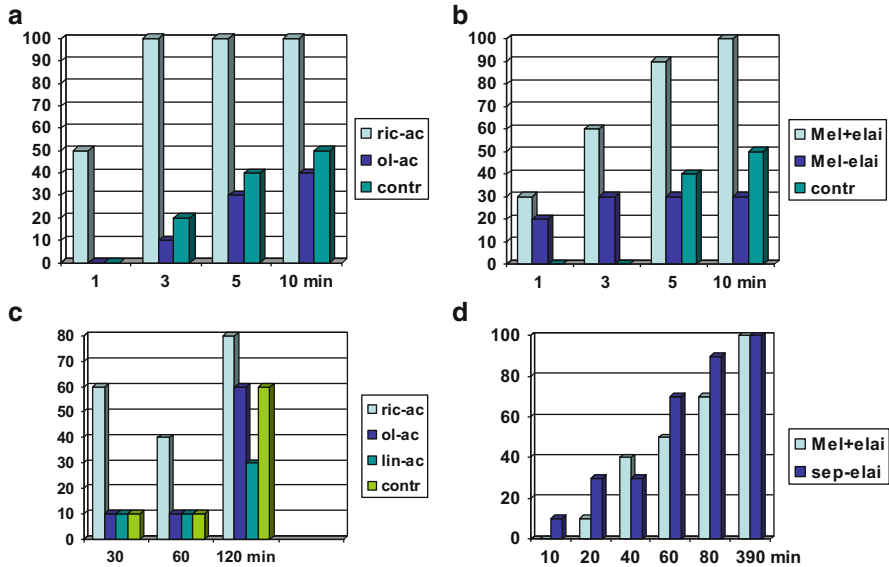


Fig. 4 Transport of diaspores and of squares of filter paper incubated with fatty acids. Ordinate: share of transported items out of 10 exposed items; 60 means 6 of 10 items transported. Abscissa: time of observation in minutes. (a) Test with squares of filter paper incubated with ricinoleic acid (ric-ac) or oleic acid (ol-ac) as compared to the control (squares not incubated) in a laboratory nest of *Lasius fuliginosus* (Bresinsky 1963). (b) Transport of diaspores of *Melica nutans* with elaiosome (= Mel + elai) and without elaiosome (= Mel – elai) as compared to blank squares of filter paper (= contr) in a laboratory nest of *Lasius fuliginosus* (Bresinsky 1963). (c) Test with squares of filter paper incubated with ricinoleic acid (ric-ac) or oleic acid (ol-ac) or linolenic acid (lin-ac) as compared to blank squares (not incubated = contr) in a laboratory nest of *Lasius fuliginosus* (Bresinsky 1963). (d) Field experiment with diaspores of *Melica uniflora*, exposition of diaspores with elaiosome (= Mel + elai), separated elaiosomes (= sep-elai). Not any of the control items (diaspores without elaiosomes) were transported by ants during the whole time of the experiment (Semander 1906)

2.4.2 Sugars

Though being found as regularly occurring compounds in the elaiosomes of nearly all of the investigated species in significant concentrations, sugars in elaiosomes (Bresinsky 1963) did not find much attention in later studies. Neglect of this aspect up to the present (except in Fischer et al. 2008) is hard to understand. First vague assumptions in respect to the presence of sugars in elaiosomes have been given by two of the early authors (Ulbrich 1919; Uphof 1942). Sugars in elaiosomes are in the order of their frequency glucose, fructose, sucrose and rather rarely xylose (Bresinsky 1963). Ants are not interested in the occurring pentose xylose, whereas the concentrations of hexoses (glucose, fructose) and those of the disaccharide (sucrose) in elaiosomes are high enough to draw their interest on. The concentration of the sugars in elaiosomes is much higher than their threshold value. In some of the elaiosomes the concentration of sugars is even high enough (*Iris ruthenica*, *Galanthus*) to be noticed as sweet taste by the less sensitive human tongue.

A special case is realised in *Primula vulgaris*. The seeds of this plant are equipped with elaiosomes. The diaspores are exposed in capsules opening close above the ground. The elaiosomes contain lipids, and glucose in low concentration just to be detectable. The seeds get separated from the central placenta at the time of fruit maturation. They remain in dense clusters within the opened capsule. At this time the placenta secretes a liquid containing sucrose, glucose and fructose. Again the concentration of the diluted sugars is high enough to be noticed by the human tongue. Finally the seeds get coated by the sweet liquid like a frosting. These observations agree with the fact that the just opened capsules of the plant (still fixed to it) are already visited by ants (Sernander 1906; Bresinsky 1963) and that even seeds with removed elaiosomes are transported by them (Sernander 1906). Non-myrmecochorous species of the same genus *Primula* (*P. elatior*, *P. veris*) with fruits on elevated stems have no elaiosomes and the placenta does not secrete a sweet liquid containing sugars.

The role of sugars in elaiosomes in comparison to lipids has to be tested experimentally. Appropriate experiments remain to be done. Judging from the occurrence of lipids and sugars in elaiosomes in regard to their respective attractiveness to ants, only indirect conclusions can be drawn based on the following observations. As elaiosomes of some myrmecochorous plants contain lipids, but no sugar (as in *Chelidonium* spec.), and on the other side some non-myrmecochorous species have seeds with appendages that contain sugar but no lipids (*Colchicum* spec.) it can be deduced that sugars alone, if not present in higher concentrations (i.e. not above the threshold value to a considerable extent), do not contribute essentially to myrmecochory. However, if the concentration of sugars in elaiosomes and on the seed coat is high enough, then myrmecochory might be triggered by the presence of sugars alone as in *Primula vulgaris*. In the elaiosomes of *Melica nutans* no lipids in form of triglycerides were found histochemically, but sugars were detected. Nevertheless, the situation in *Melica nutans* should not be compared with the situation in *Primula vulgaris* because lipids are obviously present as free fatty acids in elaiosomes of *Melica* (Bresinsky 1963).

2.5 *Advanced Studies on Myrmecochory*

The studies which followed the publication of Marshall et al. (1979) brought to light several new aspects in regard to myrmecochory.

Ants react differently if they are confronted with diaspores of different types with or without elaiosomes. Their behavioural pattern includes ignoring, eating the elaiosome in situ, transport of the diaspores directly to the refusal area of the ant's nest, transport into the nest (foraging, feeding), or information of other workers for support in transport activity (recruitment). For each of these behavioural reactions special releaser compounds are postulated. The fate of a diaspore after coming into contact with an ant would more or less strictly depend on specific chemical elicitors in the elaiosome which cause a special reaction such as eating, feeding, necrophoric

behaviour, foraging or recruitment (Bradshaw and Howse 1984). This idea is contradicted by the observation that two different kinds of transport (necrophoric or foraging) are triggered by oleic acid anyway; its outcome depends on the main current activity in which the ants are engaged in the nest (Gordon 1983).

Diaspores equipped with elaiosomes are carried into the nest by ants for feeding their larvae. After feeding, the diaspores being deprived from their elaiosomes (however, with the intact embryo being still embedded in the seed) are disposed in deeper parts of the nest or on refusal piles outside the nest. In labelling experiments it has been shown that the rate of uptake of nitrogen and carbon originating from elaiosomes is considerably higher in the ant's larvae (61 %) than it is in the workers (39 %) of a colony (Fischer et al. 2005).

The possible advantages for the plant are manifold (Beattie 1985). Different variants of a selective advantage are discussed (Hölldobler and Wilson 1990; Giladi 2006; Fokuhl 2008): directed dispersal of diaspores to suitable places for germination of seeds and for the establishment of progeny, migration over certain distances, protection from losses through feeding animals and some other advantages.

The importance of the diglyceride 1,2-diolein as an elicitor of transport activity was also confirmed in case of the ant species *Pogonomyrmex rugosus*. This observation agrees well with the fact that the mentioned compound is present in the elaiosomes of the North American *Hepatica americana* (Skidmore and Heithaus 1988). Lipid fractions obtained from the elaiosomes of this plant were tested in a bioassay using the mentioned ant species. The distances of diaspore transport by the ants were determined. The highest transport rates were observed using intact seeds, isolated elaiosomes, crude extracts of non-polar lipids and diglycerides containing fractions from the TLC separation of lipids. Transportation rates were remarkably lower, however still moderate, if the ants were confronted with test items containing mixtures of polar and non-polar lipids or with free fatty acids (exclusive ricinoleic acid which could not be traced in the elaiosomes of *Hepatica americana*). Transportation rates were definitely low or nearly zero in case of test items containing monoglycerides and triglycerides, or if blank test items (without lipids or other compounds) were offered. The reaction of ants in the time after release of diaspore transport should be differentiated from other behavioural patterns. A possible behavioural attitude of eating immediately would prevent the transportation of diaspores. The release of necrophoric behaviour would only result in removing diaspores out of the nest but not in transport to the nest. Taking this into account there are only two remaining possibilities which could be decisive for the success in dispersal. Compounds within the elaiosomes could release either a behaviour similar to that directed towards the animal prey (arthropods) of ants or a brood-tending behaviour which would also afford a transport activity to the nest (Carroll and Janzen 1973; Horvitz and Beattie 1980; Skidmore and Heithaus 1988). Triolein (triglyceride) and diolein (diglyceride) elicit brood-tending behaviour whereas free oleic acid remains without response in workers of the fire ant *Solenopsis invicta*. Triolein has been identified as a brood pheromone in this ant species (Bigley and Vinson 1975).

The investigation of the differently equipped elaiosomes of three species of *Trillium* (occurring in North America) in respect to their attractiveness towards the ant species *Myrmica punctinervis* permitted an estimation about the value of characters (even if competing with each other) being effective for seed dispersal (Lanza et al. 1992). It is not so much the dimension of an elaiosome, even not a maximal high share of lipids in the spectrum of compounds stored in the elaiosome, rather than the offer of special free fatty acids which is decisive for releasing the transport activity. Oleic acid in higher concentrations present in elaiosomes was shown to promote a strong interest of the ants towards such items. However, higher rates of transport were observed if elaiosomes contained instead of oleic acid a higher share of other free fatty acids. As a matter of fact, linoleic acid was considered to trigger the transportation of seeds (Lanza et al. 1992). It is also linoleic (and linolenic) acid, as a component in triglycerides and as a free fatty acid as well, which is a phagostimulant in the omnivorous ant species *Solenopsis saevissima* (Vinson et al. 1967). These observations and conclusions of the above-mentioned authors eventually limit to some extent the general validity of the results obtained by Marshall et al. (1979).

The response of ants belonging to different nutritional groups towards elaiosome-equipped diaspores is different, depending on the compounds within the elaiosomes. In regard to the fate of diaspores, granivorous ants (like *Tetramorium caespitum*) have to be distinguished from so-called mutualistic species (*Myrmica ruginodis*) which treat diaspores with care and dispersing them without setting damages to the germ. The differences in behaviour of both nutritional groups of ants have been investigated by Gammans et al. (2006) using the seeds of two species of *Ulex*. Different from elaiosomes of most of the other species these are of yellow colour. As expected, the experiments revealed that the colour is not important for the perception of the elaiosomes by the ants. Granivorous ants apparently come into contact only mechanically with the items of their interest. Towards free fatty acids and other lipids no remarkable reactions were observed. Mutualistic seed dispersing ants, however, take interest in the lipids on the surfaces of the diaspores and elaiosomes with the final result of transport. In the *Ulex*-*M. ruginodis* interrelationship the diglycerides only mediate the first contacts of ants with the diaspores. The elicitation of diaspore transport depends on other compounds with which the ants presumably come into contact after biting into the elaiosomes. Different from the results of Marshall et al. (1979) obtained for *Hepatica americana* the diglycerides of elaiosomes in *Ulex* are not dominated by oleic acid (present only in small quantities) but rather by palmitic acid, stearic acid and arachidic acid. The elaiosomes contain four essential fatty acids (such as linoleic and linolenic acid) and four essential sterols which are required for raising the breed (Gammans et al. 2005).

A variation in the chemical composition of elaiosomes is not only apparent in different genera or species of myrmecochorous plants but also if different provenances within a species are compared to each other (Boulay et al. 2006; Boieiro et al. 2012). In *Helleborus foetidus* the quantities of triglycerides, diglycerides and free fatty acids were different in elaiosomes from distant

(750 km) growing populations (Boulay et al. 2006). The variation was correlated with different attractiveness of the diaspores in respect to ants. The elaiosomes originating from one place were more attractive to ants, especially towards the ant species (*Formica lugubris*), showing a high activity in that area, as compared to the elaiosomes of the other locality with other species of ants (*Aphaenogaster iberica*, *Campanotus cruentatus*) being there most frequently engaged in transport of diaspores. The elaiosomes of higher attractiveness were characterised by their somewhat bigger dimensions (so also according to Mark and Olesen 1996) and by a higher share of oleic acid as compared to the share of palmitic acid and linoleic acid, whereas the share of diglycerides remained equal. In a bioassay dummies soaked with triglycerides, diglycerides or free fatty acids were evidently preferred to be transported by *Aphaenogaster iberica* as compared to the control (only treated with the solvent). Dummies treated with extracts of triglycerides or with diglycerides were not differently transported by the ant species.

On the other side in a pairwise competition test, dummies treated with free fatty acids obtained from the attractive elaiosomes were transported at a higher rate than those with fatty acids from the less attractive ones. The higher attractiveness is obviously associated with the fraction of free fatty acids and is presumably due to a higher content of oleic acid (in the fraction of free fatty acids and also as component of triglycerides and diglycerides). These observations point to regionally differing selective pressures in regard to the chemical composition of elaiosomes (Boulay et al. 2006). Putative adaptations of the dimensions and of the weight of diaspores of *Helleborus* in regard to the size of the involved species of ants were not clearly evident (Garrido et al. 2002).

An indirect evidence for the adaptive value of elaiosomes in regard to the dispersal of diaspores has to be seen in the fact that the composition of compounds accumulated in elaiosomes on one side and in the seeds (without elaiosomes) on the other side is quite different (Boulay et al. 2006; Fischer et al. 2008; Boieiro et al. 2012). The share of myrmeco-attractive lipids in elaiosomes (e.g. oleic acid) and the concentration of soluble carbohydrates (fructose, glucose, sucrose) are higher in elaiosomes than in the corresponding seeds. Differences in composition were also observed with regard to the contents of free amino acids, especially regarding the share of histidine with a 7.5 times higher concentration in elaiosomes as compared to the seed (Fischer et al. 2008). Taking these results into account the nutritive value of elaiosomes as source of nitrogen might be much higher than previously accepted (Bresinsky 1963). The significance of elaiosomes for nursing the brood of ants (as stated by Beattie 1985 for ant colonies in general) was recently proved in experiments (Gammans et al. 2005; Fokuhl 2008; Fokuhl et al. 2007, 2012). A mutualistic interrelationship between ants and myrmecochorous plants is also somewhat supported by the observation of a higher germination rate of seeds (f. i. in 8 of 28 tested species) after having been deprived of their elaiosomes (Horvitz and Beattie 1980; Fokuhl 2008).

An excellent survey on myrmecochory (Mayer et al. 2005) summarises the still existing demands on future research as follows: (1) What is the effect of elaiosomes on ant-colony demography? (2) What is the effect of ant dispersal on plant species