Functional Surfaces in Biology
Functional Surfaces in Biology

Little Structures with Big Effects

Volume 1

edited by

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Abstract

Biological surfaces represent the interface between living organisms and the environment and serve many different functions: (1) They delimit the organism, give the shape to the organism, and provide mechanical stability of the body. (2) They are barriers against dry, wet, cold or hot environments. (3) They take part in respiration and in the transport of diverse secretions, and serve as a chemical reservoir for the storage of metabolic waste products. (4) A variety of specialised surface structures are parts of mechano- and chemoreceptors. (5) The coloration and chemical components of surfaces are important components for thermoregulation, and are often involved in diverse communication systems. (6) A number of specialised surface structures may serve a variety of other functions, such as air retention, food grinding, body cleaning, etc. In spite of a huge number of publications, describing biological surfaces by the use of light and electron microscopy, exact working mechanisms have been clarified only for a few systems, because of the structural and chemical complexity of biological surfaces. However, biological surfaces hide a virtually endless potential for technological ideas for the development of new materials and systems. Because of the diversity of functions of biological surfaces, inspirations from biology may be interesting for a broad range of topics in engineering sciences: adhesion, friction, wear, lubrication, filtering, sensorics, wetting phenomena, self-cleaning, anti-fouling, thermoregulation, optics, etc. Since the majority of biological surfaces are multifunctional, it makes them even more interesting from the point of view of biomimetics. In the present book, some structural aspects of biological surfaces in relation to their function are reported. The editor and contributors believe that such a functional approach to biological surfaces will make this book interesting not only for biologists, but also to physicists, engineers and materials scientists.
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Introduction
Introduction: Surface Properties and their Functions in Biological Systems

Stanislav Gorb

Biological surfaces represent the interface between living organisms and the environment and serve many different functions. (1) They may delimit dimensions, often give the shape to organism, and provide mechanical stability to the body. (2) They are barriers against dry, wet, cold or hot environments. (3) They take part in respiration and in the transport of diverse secretions, and serve as a chemical reservoir for the storage of metabolic waste products. (4) A variety of specialised surface structures are parts of mechano- and chemoreceptors. (5) Optical properties may contribute to thermoregulation and the physical coloration pattern is often involved in diverse communication systems. (6) A number of specialised surface structures may serve a variety of other functions, such as air retention, food grinding, body cleaning, etc. (Gorb 2005).

The biological world is part of the physical world and, therefore, physical rules are also applicable to living systems. Living creatures move on land, in the air, and in water. There are complex motions inside their bodies to provide fluid circulation or to generate forces for locomotion. The resistance against motion mediated by surrounding media and by mechanical contact with various substrates was an evolutionary factor which contributed to the appearance of many surfaces adapted to reduce such resistance. On the other hand, some surfaces bear different mechanisms related to optics: reflection reduction, generation of colour due to a particular micro- and nanostructure pattern. Small surface structures at the micrometer and nanometer scales are often vitally important for a particular function or a set of diverse functions.

There are numerous publications describing biological surfaces using light and electron microscopy. Because of the structural and chemical complexity of biological surfaces, exact working mechanisms have been clarified only for some systems. Since all biological surfaces are multifunctional, it makes them even more interesting from the point of view of biomimetics. In the present volume, we discuss some functions of biological surfaces and their relationship with the structure. The volume is subdivided into the following topics: (1) Protection and defence (two chapters),

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(2) Anti-wetting (five chapters), (3) Transport (one chapter), (4) Aerodynamics (one chapter), (5) Acoustics (one chapter), (6) Sensory systems (one chapter), (7) Optics (four chapters).

This volume begins with a chapter by A. Kreitschitz on the variety of functions of the plant seed slime envelope. The envelope plays an essential role in seed dispersal and creates conditions suitable for germination (either stimulation or inhibition depending on environmental cues). By adhesion of the diaspore to the soil, it is protected from unwanted moves to unfavourable habitats. By anchoring the seed in substratum, it regulates its orientation and root penetration. Additionally, the slime envelope supplies the embryo and developing seedling with water and nutrients and defends it against viral or fungal pathogenic attack.

The defence function of the easily-broken, membranous cuticle of sawflies (Insecta, Hymenoptera) is discussed in Chapter 2 by J.-L. Boevé. The so-called “easy bleeding” phenomenon is the capability of the body surface of some ten-thredinid larvae to be easily damaged. This defence strategy includes, in addition to micro-morphological characters of the surface, some behavioral, chemical, and physiological traits.

The section on anti-wetting and self cleaning is represented by five chapters devoted to various organisms and begins with the chapter by U. Hiller on the anti-wetting function of the reptilian skin. The author has studied gecko-skin that is covered by a pronounced keratinized uppermost layer, protecting the body from both extensive transcutaneous water loss and mechanical damage. Additionally, geckos possess micro-structured surfaces affecting its superhydrophobic and self-cleaning properties.

In Chapter 4, P. Perez-Goodwyn shows that, in the evolution of water bugs, different functional requirements have resulted in the appearance of structures adapted to either submersion resistance or waterproofing. In the case of waterproofing, large and stable setae at a relatively low density promote fast runoff of water. The submersion resistance function is fulfilled by long and thin setae or microtrichia in a compressible bubble, or by short, thin, densely packed microtrichia, as in the case of a plastron. An optimal compromise between these two extremes is a combination of long and stable setae and an underlying cover of thin microtrichia.

Spiders also bear hairy, water repellent surfaces described in Chapter 5 by G.E. Stratton and R.B. Suter. The authors show that water repellency not only varies widely among spider species, but also within an individual across its ventral topography, and that the support of respiratory and other functions (e.g., defence against pathogen intrusion) by hair-bearing cuticle is likely to have played an important role in the evolutionary history of spiders.

In plants, epicuticular wax crystals sometimes combined with trichomes or cuticular folds, also lead to the effect of water forming spherical droplets that bounce and roll off the surface even at the slightest inclination. This amazing water-repellency is caused by hydrophobic chemistry, together with a micro- and nanostructure of the plant’s surfaces. Such a superhydrophobicity of plant surfaces correlates with their self-cleaning properties. Although self-cleaning properties of plants have already been described as Lotus-Effect (Barthlott and Neinhuis 1997) and even transferred from biological models to technical applications, the underlying physical principles
of superhydrophobic surfaces are quite complex and offer another interesting application that has not yet been considered: water-repellent surfaces keeping air under water and even reducing drag in mobile objects. In Chapter 6, Z. Cerman, B.F. Striffler and W. Barthlott discuss the *Salvinia* plant as a possible model for technical submerged surfaces, and provide information about recent advances in the interpretation of physical and chemical basics of plant superhydrophobicity.

Some insects have developed a solution similar to plant wax crystal coverage. The particles (brochosomes) formed on the integument of leafhoppers from the family Cicadellidae create a superhydrophobic surface, apparently due to the complex fractal geometry of their surface at the micron-to-nanometer scale (Chapter 7 by R. Rakitov). These coatings serve multiple biological functions analogous to those of crystalline wax coatings of other insects and plants. At the same time, among several such functions hypothesized, only protection of the integument from wetting by water and the leafhoppers’ own liquid excreta can explain the nearly universal occurrence of brochosomes in such a diverse leafhopper family as Cicadellidae.

Wetting phenomena are also of crucial importance for plant water supply. Surface microstructures are responsible for the functionality and integrity of water transport under tension. This transport mechanism allows for water flowing through the plant. The ultimate need for coping with bubbles and embolisms is of significance for the functionality of plant water-transporting structures, and was identified as a main driving force for xylem evolution (Sperry 2003). The interrelationship between xylem structure and water transport function is documented by the fact that the earliest tree, *Archaeopteris*, bears a xylem which is very similar to modern wood. It is very probable that the surface effects, described by A. Roth-Nebelsick in Chapter 8, were already at work in this ancient taxon. It is therefore to be expected that more surface-related adaptations can be found which are of biophysical relevance for maintaining the water flow.

Feathers have been an essential preadaptation of reptiles and ancient birds to the evolvement of the flight ability. Material properties and microstructure of feathers also in recent birds are responsible for aerodynamic activity of the feathers. The origin of feathers and their microstructures remained an unresolved question, which is discussed in details by L. Alibardi in Chapter 9.

An important general question about biological surfaces is the multifunctionality of surface microstructures and change of their functions due to small changes in the geometry. As it will be shown in the final section of the book, devoted to the optical effects, the scales of Lepidoptera are famous for specialized surface structures that interact with light to produce colour. Such scales occur in a variety of butterfly and moth species, and, like other scales and bristles of the arthropod cuticle, develop from a single epidermal cell (Ghiradella 1994). An unusual function of butterfly scales, namely the production of acoustic signals is reported for male moths of the Uraniidae family (Chapter 10 by A. Barro, M. Vater, M. Pérez and F. Coro). The sound emission organs of males in three *Urania* species are situated on the prothoracic legs and consist of two zones of specialized scales located on opposite sides of the coxa and the femur of each foreleg. On the external side of the coxa, opposite the femur, there is a peg which consists of a bundle of elongated scales that are hooked at the tip. In the proximal part of the femur, in front of the peg, there
is a shallow concave surface, densely covered with scales that differ from scales on other parts of the femur (Lees 1992). The sound emission organ of Urania moths is discussed in the context of independently evolved lepidopteran sound producing surfaces that can be located on the legs, the wings, the thorax and the abdomen, including the genitalia.

Filiform hairs and their sockets on cerci of Grillus bimaculatus crickets are mechanically coupled to much smaller campaniform sensilla. Chapter 11 by R. Heußlein, H. Gras and W. Gnatzy demonstrates that strong deflection of the hair shaft parallel to the longitudinal axis of cercus causes tilting of the socket. Also, the sickle shaped area of thin cuticle around the large sockets of filiform hairs (with long hair shaft) is deformed for as long as the socket is deflected toward the cercus tip. The coupling of filiform hairs with campaniform sensilla creates a composite mechanoreceptor with an extended working range, with some limitations on the precision of directional and intensity coding.

Structural colours are the result of the interaction of light with physical structures, now generally termed photonic crystals, which are in the surface of a substratum. Such colours usually cause bright directional effects as opposed to chemical pigments, which scatter light diffusely. Structural coloration, due to the presence of scales and bristles, is well-known in insects, such as butterflies and beetles. The last section of the book consists of four chapters devoted to this topic. The most interesting type of structural coloration is so-called iridescence, which is well known in insects and birds, and has been characterized for many different species. Iridescence is a result of optical interference within multilayer structures, which are rather complex in their architecture and may be incorporated into systems that can produce several different optical effects. Such effects include diffraction-assisted reflection angle broadening, structural colour mixing and polarization effects. By describing specific structural colour examples in detail, within a general context of Lepidopteran microstructure classification, Chapter 12 by P. Vukusic presents an introduction to current work on photonics in these natural systems. Chapter 15 by A. Ingram provides an overview of numerous butterfly species showing a tremendous diversity of wing scale structures coupled to underlying photonic effects.

Another interesting optical property of surface structures has been described from the insect surface. Ommatidial gratings are anti-reflective structures on the eyes of insects, especially those which are nocturnally active. These protuberances are very small microtrichia (200 nm in diameter), which increase visual efficiency through decreased surface reflection in their density, and increased photon capture for a given stimulus condition (Chapter 13 by A. Parker). Such a grating is particularly useful on a curved corneal surface, as it would increase the transmission of incident light through the cornea, compared with a smooth surface.

Animal colors have, of course, a biological meaning other than taking an observer’s fancy. Well-known biological functions for body colors are display and camouflage, both of which can be executed by pigment colors. Iridescent colors presumably always have a visual function, either to call the attention of conspecifics or to warn potential predators. Occasionally, the insect’s eyes themselves are iridescent, due to multilayers in the facet lenses. Furthermore, insect
eye surface structures employ various optical methods to improve visual functions. Chapter 14 by D. Stavenga reviews surface phenomena, not only from a purely optical viewpoint, but also considering their visual and biological functions.

Unfortunately, it was not possible to include all chapters on interesting surface structure-function effects in one volume. For this reason numerous contact mechanics effects related to friction and adhesion can be found in Volume 2: Functional Surfaces in Biology: Adhesion Related Phenomena.

The two volumes on Functional Surfaces in Biology taken together, present an overview of current research activities on functions in various biological surfaces. They provide a reference for a novice in the field. The chapters generally have an overview along with new research data. The volumes are also intended for use by researchers who are active, or intend to become active, in the field. The appeal of this topic is expected to be broad, ranging from classical biology, biomechanics and physics to surface engineering.

References


Protection and Defence
Chapter 1
Biological Properties of Fruit and Seed Slime Envelope: How to Live, Fly, and Not Die

Agnieszka Kreitschitz

1.1 Introduction

Slime (mucilage, mucous material) commonly occurs in nature in numerous groups of plants. Its presence has been detected in such different organisms as algae, lichens, mosses and ferns, as well as in many representatives of gymnosperms and angiosperms (Grubert 1974, Mouradian 1995). In the latter group of plants, the ability to produce mucilage is a characteristic of both vegetative and generative organs, including leaves, entire shoots, roots and flower elements (Broda 1948, Mollenhauer 1966, Garwood 1985, Gregory and Baas 1989). Usually, a group of cells or single cells are involved in the production of slime; rarely, specialised tissue participates in this process (Mühlthaler 1950).

The ability to synthesize mucilaginous substances is a striking feature of diaspores (fruits and seeds) in many flowering plants. It has been reported for more than 80 families of dicotyledonous plants, including Brassicaceae, Linaceae, Malvaceae, Lamiaceae, Euphorbiaceae, Plantaginaceae, Acanthaceae and Asteraceae (Wojciechowska 1961, Gutterman et al. 1967, Swabrick 1971, Vaughan et al. 1971, Grubert and Hambach 1972, Korobkov 1973, Young and Evans 1973, Grubert 1974, Witztum 1978, Oganesova 1981, Baiges and Blanché 1988, Baiges et al. 1991, Mouradian 1995, Huang and Gutterman 1999a, b, Huang et al. 2000, Yakovleva et al. 2002, Mosquero et al. 2004). The coat of myxospermatic (mucilaginous) diaspores\(^1\) usually comprises at least two different types of cells: the proper epidermal cells and the slime cells that, to a different degree, cover the surface of the seed or fruit (Wojciechowska 1961, 1966, Korobkov 1973). Slime cells can be distributed in the epidermis or in subepidermal layers. In addition, whole structures, e.g. mucilage-epidermis (Polemoniaceae, Lamiaceae) or mucilage hairs (Cobea scandens; Grubert 1974), can be responsible for slime production.

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\(^1\) Myxospermatic diaspores – dispersal units, such as anthocarps, fruits, seeds and embryos become mucilaginous after being wetted (Grubert 1974).
Due to the presence of slime cells and the specific chemical composition of their cell walls, dry diaspores quickly form a mucilaginous envelope when wetted (Mühlethaler 1950, Fahn and Werker 1972, Grubert and Hambach 1972, Grubert 1974, 1980, Gutterman and Shem-Tov 1997, Gutterman 2000, Windsor et al. 2000, Yakovleva et al. 2002). The occurrence of such slime-forming seeds and fruits is considered an ecologically important adaptive trait in arid environments, which is particularly well developed in plants inhabiting deserts, semi-deserts, and steppes (Vaughan et al. 1971, Young and Evans 1973, Baiges and Blanché 1988, Gregory and Baas 1989, Baiges et al. 1991, Huang et al. 2000). In such extreme habitats, the slime envelope surrounding a diaspore is undoubtedly beneficial for plants. It inhibits or stimulates germination by means of water retention, facilitates adhesion to the ground (thus preventing transportation to unfavorable habitats) or by adhesion to an animal’s body (which plays a key role in long-distance diaspore dispersal) (Witztum et al. 1969, Fahn and Werker 1972, Young and Evans 1973, Werker 1980/81, Baiges et al. 1991, Gutterman and Shem-Tov 1997, Huang and Gutterman 1999a, Gutterman 2000, Huang et al. 2000, 2004). The slime envelope may also have additional protective functions. Thus the ecological benefits coming from the presence of the slime envelope cannot be overestimated in such environmental conditions.

1.1.1 Chemical Composition of the Slime

Slime belongs to complex carbohydrates. Pectins, which are mostly polymers of galactouronic acid residues, are slime’s main component. They have an especially strong capacity for hydration and after wetting form a gel-like envelope (Frey-Wyssling 1959, Fahn and Werker 1972, Western et al. 2000, 2001, 2004, Huang et al. 2004). The presence of rhamnose (Frey-Wyssling 1959, Western et al. 2000, 2004, Penfield et al. 2001, Willats et al. 2001) and other monosaccharides, such as glucose and fucose, are shown to exist in slime of Arabidopsis seeds (Western et al. 2000). Moreover, arabinose, xylose, galactose, and mannose have been found in the mucilage of yellow mustard (Sinapis alba; Cui et al. 1993). Many other chemical compounds have also been detected in slime of different species (Broda 1948, Warrand et al. 2005).

The slime forms a colloidal solution which regulates physical and chemical conditions, e.g. viscosity, pH of the environment, electric charge, surface tension and conductivity, which is necessary for the proper development and functioning of the seed and the entire plant (Broda 1948).

Classification distinguishes “true slime” as a consisting of almost exclusively of pectins, which occurs e.g. in Linum usitatissimum (Mühlethaler 1950), and cellulosic slime, e.g. in Cydonia vulgaris (Mühlethaler 1950, Abeysekera and Willison 1987), Collomia grandiflora (Schnepf and Deichgräber 1983a), Salvia spp. (Mühlethaler 1950), Cobeascandens (Mühlethaler 1950, Frey-Wyssling 1959) or Artemisia spp. (Yakovleva et al. 2002, Kreitschitz and Vallès 2005, 2007). The distinct feature of the latter slime type is the additional presence of a cellulosic
The difference between “true” and cellulosic slime is not only structural, but the occurrence of cellulose fibrils has a functional significance. It is possible that cellulose threads increase the degree of adhesion and anchor the diaspore, thus helping in the root's penetration of the soil (Gutterman et al. 1967). The presence of such cellulosic fibrils makes slime more rigid and results in closer contact between the mucilage coat and diaspore (Grubert 1974).

Particular properties of slime compounds can be visualized by specific microstaining reactions, for example, safranin provides a very strong staining reaction for pectins (Fig. 1.1a). While another dye, ruthenium red, typically used to stain pectins, reveals their homogenous structure (Fig. 1.1b; Filutowicz and Kuźdowicz 1951, Broda 1971, Western et al. 2000, 2001, 2004). Conversely, staining with methylene blue (Figs. 1.1c, d, and 1.2e), safranin (Fig. 1.2a) or I in KI + H₂SO₄, reveals the cellulose component (Johansen 1940, Filutowicz and Kuźdowicz 1951, Broda 1971, Gerlach 1972, Braune et al. 1975).

Cellulose spirals, in some cases, can also be visible when unstained. For instance, unicellular mucilaginous trichomes, present on the fruit surface of Cobea scandens [viewed in the scanning electron microscope, SEM (Fig. 1.1e, Fig. 1.2d), or light microscope (Figs. 1.1f and 1.2b)], possess distinct spirally coiled threads (Quader et al. 1986).

### 1.1.2 Subcellular Localization of the Slime

Slime is, in most cases, deposited in the last stage of protoplast life between the primary cell wall and the plasma membrane. Further chemical changes and dehydration during diaspore maturation finally shape the slime layer (Van Caesele et al. 1981, Werker 1980/81, Abeysekera and Willison 1987, Western et al. 2000, Windsor et al. 2000, Penfield et al. 2001). However slime formation rarely results from the secondary modifications in the cell wall (Fahn and Werker 1972).

The thickness of a slime layer usually differs within the cell, typically with the outer cell wall adcrusted, as in Arabidopsis thaliana (Beeckman et al. 2000, Windsor et al. 2000), Brassica campestris (Van Caesele et al. 1981) or Cydonia vulgaris (Mühlthaler 1950). However, all cell walls can undergo a process of thickening, e.g. in representatives of Linum and Cannabis (Mühlthaler 1950).

In the cellulosic type of slime, cellulosic fibrils may be deposited either as the primary, e.g. in Lepidium sativum (Frey-Wyssling 1959) or as a secondary cell wall, e.g. in Cobea scandens (Mühlthaler 1950, Frey-Wyssling 1959, Fahn and Werker 1972, Quader et al. 1986), and in representatives of Collomia (Barthlott 1981, Schnepf and Deichgräber 1983b), Ruellia (Grubert 1974, Barthlott 1981, Schnepf and Deichgräber 1983b) and Artemisia (Grubert 1974, Kreitschitz and Vallès 2005, 2007). Often the cellulose fibrils are clearly visible as annular or spiral secondary thickenings (Fig. 1.2a, b; Frey-Wyssling 1959, Fahn and Werker 1972, Gutterman et al. 1973, Grubert 1980, Werker 1980/81, Schnepf and Deichgräber 1983a, b).
1.1.3 Distribution of Slime Cells on the Fruit and Seed Surfaces

Generally a diaspore coats consist of the proper epidermal cells and those producing the mucilage, which are the slime cells (myxogenous, mucilaginous) cells. These can be distributed in different ways on fruit or seed surfaces. The slime cells can...
be arranged in stripes of different widths, e.g. in \textit{Prunella} (Wojciechowska 1961, 1966, Mosquero et al. 2004), or in isolated rows, as in \textit{Anthemis}, \textit{Artemisia}, and \textit{Matricaria} (Grubert 1974). Often they are restricted to the margin of the seed, e.g. in \textit{Selliera radicans} (Grubert 1974) or can assemble groups of a few cells scattered among non-mucilaginous epidermal cells, such as in \textit{A. nova} (Kreitschitz and Vallès 2005, 2007). The diaspore surface can also be entirely covered by slime cells, e.g. in \textit{Cleonia lusitanica} (Wojciechowska 1961, 1966, Mosquero et al. 2004),
Plantago media (Fig. 1.2c; Kreitschitz unpublished data) and in numerous taxa of Brassicaceae (Vaughan et al. 1971, Werker 1980/81). In some cases, slime hairs cover the whole seed surface, such as in Cobea scandens (Fig. 1.2d) and in other taxa from the genera Hygrophila, Ruellia or Blepharis (Gutterman et al. 1967, 1973, Grubert 1974, Schnepf and Deichgräber 1983b, Quader et al. 1986).

The microsculpture of the diaspore coat provides additional information about the abundance of slime in relation to environmental conditions. A smooth or non-sculptured surface typically occurs in plants growing in habitats sufficiently supplied with water; conversely, well-developed distinct sculpturing is characteristic of xerotermic species with myxospermatic diaspores (Barthlott 1981).

1.1.4 Slime Envelope Formation

A dry diaspore placed in water rapidly hydrates due to a pectin matrix presence, and within a few seconds forms a gel-like envelope (Wojciechowska 1966, Fahn and Werker 1972, Grubert and Hambach 1972, Grubert 1974, Huang and Gutterman 1999b). If a cellulosic type of slime is produced, then the cellulose skeleton is released together with pectins (Fahn and Werker 1972, Grubert and Hambach 1972, Kreitschitz and Vallès 2007). It frequently has the shape of spirally coiled threads, e.g. in Collomia grandiflora (Grubert and Hambach 1972). The cellulose fibrils can uncoil, noticeably increasing their length and form a hedgehog-like shaped envelope around the diaspore, e.g. in Conringia orientalis, Euphorbia falcata (Grubert 1974), Salvia sp. (Fig. 1.2e, Kreitschitz, unpublished data), Rosmarinus sp. (Fig. 1.1d, Kreitschitz, unpublished data) and some Artemisia taxa (Fig. 1.1c; Kreitschitz and Vallès 2005, 2007). The process of slime envelope formation can be so sudden that within several seconds and up to a few minutes after wetting, the diaspore becomes completely enclosed in the mucilaginous envelope.

1.2 Biological Functions of Slime: How to Live

1.2.1 Water Retention

The slime envelope is responsible for the rate, amount and time of water absorption and for the delay in the process of water loss. Due to its chemical composition, slime has a strong capacity to swell, i.e. to absorb a considerable amount of water in a relatively short time. Thus, slime-forming diaspores can accumulate and maintain water as opposed to those seeds and fruits that do not produce slime (Garwood 1985, Gutterman and Shem-Tov 1997, Huang and Gutterman 1999b, Huang et al. 2000). A striking discrepancy in water retention ability was shown for Artemisia monosperma. In this species, the weight of normal fruit (achene) increased more than 20 fold after hydration, but when the slime layer was removed experimentally, the weight increase after being wetted was only 3.5 fold (Huang and...
Gutterman 1999a, Huang et al. 2000). The extreme capacity of water absorption by the slime layer is remarkably manifested in *Artemisia sphaerocephala*. In this species, the weight of the slime envelope alone increases more than 589 times after maximum water absorption! However in the same experiment, it was shown that for another *Artemisia* species, *A. ordosica*, the weight of the slime layer increased only 27 times (Huang et al. 2000).

In addition, the loss of water by slime-forming diaspores is much slower, when compared to those devoid of slime. The return to the initial dry-weight is delayed and can last from about 6–7 hours in *Carrichtera annua* (Gutterman and Shem-Tov 1997) to more than 9 hours in *Artemisia sphaerocephala*. In the latter case, achenes with experimentally removed slime layer returned to their initial weight within two hours (Huang and Gutterman 1999b, Huang et al. 2004). The real winners, however, are the slime-forming fruits of *Cavanillesia plataniifolia*, which have an ability to retain water for almost two weeks (Garwood 1985)!

### 1.2.2 Germination: The Beginning of Life

Slime is beneficial for plants in many ways, especially helping them to survive the first sensitive stage of life – germination. In this stage the seedling requires a continuous supply of water and nutrients and adequate protection against negative abiotic and biotic influences of the environment.

Imbibition and retention of water by the slime envelope is ecologically beneficial, in particular, for plants inhabiting arid and xerothermic habitats (Fahn and Werker 1972, Korobkov 1973, Gutterman and Shem-Tov 1997, Huang et al. 2000). For these plants, water absorbed by the slime envelope is one of the most important factors regulating germination in either stimulating or inhibiting it (Fahn and Werker 1972, Young and Evans 1973, Werker 1980/81, Young and Martens 1991, Huang et al. 2000, Mosquero et al. 2004).

The slime envelope makes it possible for water to be kept around the diaspore and in this way creates favorable conditions for the acceleration of germination (Gutterman and Shem-Tov 1996, 1997, Huang and Gutterman 1999a). As was shown for *Artemisia monosperma*, achenes germinated within 16 hours, when placed in distilled water (Huang and Gutterman 1999a). Eight additional hours were necessary for myxospermatic achenes of *Artemisia sphaerocephala* to germinate (Huang and Gutterman 1999b), whereas slime-forming seeds of *Anastatica hierochuntica* were able to begin germination within 6 hours (Friedman and Stein 1980, Gutterman 1994, Shem-Tov and Gutterman 2003), and *Blepharis* spp. in 1–3 hours after wetting (Gutterman 2000)!

Aside from the actual presence of the slime envelope, the amount of water retained by it is also an important aspect. Even a scarce amount of slime helps in germination by means of seed adhesion to the soil and by creating supportive conditions, in which water diffusion from the soil to the seed is facilitated. Nevertheless, even a small excess of water in the envelope can restrain germination (Gutterman...
et al. 1967, 1969, 1973) mainly by the regulation of oxygen availability for the embryo. Swelled slime may create a special microhabitat for certain microorganisms developing in the seed coat and competing for oxygen with the embryo, thereby negatively affecting germination (Gutterman et al. 1967, 1973, Werker 1980/81). Swelled slime can be a physical barrier impermeable to oxygen, thus delaying germination in unfavorable conditions (Witztum et al. 1969). For instance, in *Blepharis persica* seeds, which are covered by long slime trichomes, additional water causes mucilage swelling which fills all the spaces between the trichomes, drastically limiting oxygen diffusion and, as a result, inhibiting germination (Gutterman et al. 1967). With an excess of water, *Blepharis* seeds do not germinate, even after additional oxygen supply. This is in contrast to seeds with the slime layer removed, which are able to germinate in conditions of low oxygen concentration (Witztum et al. 1969). It was stated that such a phenomenon has an ecological significance for diaspores dispersed by floods (Witztum et al. 1969). The role of the slime envelope as a physical barrier in a gas exchange was also reported for *Hirschfeldia incana* (Brassicaceae) (Western et al. 2000), and *Linum usitatissimum* (Kuznetsov and Hasenstein 2003).

The presence of a slime envelope, besides controlling the process of germination, can also affect further growth of a seedling. For example, young plants of *Artemisia monosperma* and *A. sphaerocephala* that developed from normal achenes were stronger and bigger than those developing from fruits with an experimentally removed slime layer (Huang and Gutterman 1999a, b). It has been suggested that an embryo can allocate not only water, but also organic compounds present in the slime envelope (Huang and Gutterman 1999a). For instance, in *Cavanillesia plataniifolia*, the occurrence of a slime envelope was obligatory for the successful expansion of cotyledons and the further growth of a seedling, especially in water deficit conditions (Garwood 1985). Additionally, slime may contain a certain amount of auxin, which is known to be a regulating factor for proper embryo development, seed germination and further seedling growth (Huang and Gutterman 1999b).

As it is shown here, the presence of a slime envelope and its properties controls the process of germination and further development of a seedling. First, the slime can be a reservoir of water as well as a means of storage of organic compounds, and indirectly, of energy. Surprisingly, the slime envelope can presumably orchestrate a type of carnivorous behavior, attracting and trapping soil organisms. Such an asset was suggested for seeds of *Capsella bursa-pastoris*, where the slime contains protease and may absorb amino acids (Barber 1978). It is also speculated that due to a similar “carnivorous” ability of the slime envelope, seedlings of *Cavanillesia plataniifolia* growing in poor tropical soils might obtain an additional supply of nutrients (Garwood 1985).

### 1.2.3 DNA Integrity and Repair

Swelling of an envelope can be triggered even with a small amount of water, e.g. by dew, yet this amount is insufficient to begin germination. Nevertheless, it can affect other processes in the embryo, such as re-establishment of cell membranes...
(Huang et al. 2004), repair, and restoration of DNA integrity (Osborne 1980/81, Osborne 2000, Huang et al. 2004). It is suggested that the maintenance of DNA integrity by the embryo assures quick germination of Artemisia sphaerocephala and A. monosperma diaspores shortly after the appearance of sufficient amounts of water. Thus, in desert habitats, in which both species occur, the presence of the slime envelope can considerably increase the endurance of the seedlings (Huang et al. 2004).

1.2.4 Light and Temperature

The process of slime swelling is associated with thermal changes within it because of the colloidal nature of the slime. During pectin hydration and water particle binding, a certain amount of heat is produced. This may increase the temperature and affect plant organ development (Broda 1948), including germination.

The slime envelope may also indirectly change thermal conditions by focusing light. As was shown for Hesperis matronalis seeds, the lens-shaped mucilaginous envelope directs light into the aleuronic layer. This facilitates germination (Grubert 1974), and possibly activates the enzymes involved in the mobilization of storage materials of the seed.

1.2.5 The Role of the Slime Envelope in the Colonization of Extreme and Disturbed Habitats

Formation of a slime envelope by a diaspore is beneficial not only for plants growing in areas with limited access to water, but it is also advantageous for colonizing specific places, such as ruderal and disturbed habitats. Slime-forming fruits and seeds are typical of many common weeds growing in such places, e.g. Lepidium flavum, L. nitidum, Plantago lanceolata, Cardaria draba (Young and Evans 1973) and Arabidopsis thaliana (Western et al. 2000). In these plants, formation of the slime envelope speeds up germination and the development of seedlings. Diaspores do not have to be covered by soil to be able to germinate because the mucilaginous layer on the surface of the coat protects them from drying out (Young and Evans 1973).

Production of slime by diaspores is also a common strategy in annual plants that frequently occur in extremely arid and/or disturbed environments (Gutterman 2000, Young and Evans 1973). Many myxospermatic taxa are annual plants with a short life cycle that has to be accomplished over a few weeks or months. For these plants, the presence of slime is particularly important, as it helps in quick germination and makes colonization of a new habitat prior to the appearance of other competing species possible (Sorensen 1986). A comparison of Dracocephalum taxa (differing in duration of the life cycle) revealed slime occurrence in biennial plants (D. thymiflorum, D. nutans) as opposed to perennial species (D. Ryischiana, D. peregrinum) that did not show an ability to produce mucilage (Grubert 1974).