Review

More than just a coating: Ecological importance, taxonomic occurrence and phylogenetic relationships of seed coat mucilage

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ABSTRACT

Studies on the ecological importance of seed coat mucilage have provided valuable information about its roles in critical stages of the plant life cycle. Seed mucilage may, by providing a moist environment and maintaining metabolic activity in the seed, promote seed development. In seed dispersal, seed mucilage influences topochory, epizoochory, endozoochory and hydrochory by anchorage of seeds to soil surface, lubrication or changing the specific weight of the seed. In arid environments, seed mucilage can prevent seeds from drying or initiate DNA repair mechanisms, thereby maintaining the soil seed bank. Seed mucilage reduces oxygen diffusion to the seed and thus has a role in regulating seed dormancy. Due to it being hydrophilous, acting as a physical barrier and containing chemicals, seed mucilage is proposed to promote seed germination in favorable environments. In seedling growth, seed mucilage may lubricate the radicle as it penetrates the soil and be degraded by soil microfloras and thus promote seedling growth. Further investigation of seed mucilage for more species in diverse habitats from the perspectives of evolution, genetics, proteomics, phylogeny and plant–microbe interactions would contribute substantially to our understanding about its ecological importance.

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Introduction

The external surface of seed and fruit coats of angiosperms is extremely diverse, reflecting multiple adaptations to environmental conditions. Upon imbibition of water, seeds or fruits of many species produce a pectinaceous mucilage (myxodiaspory). Mucilage has been reported to be produced by seeds or fruits of species in 37 orders, 110 families and at least 230 genera of angiosperms (Supplementary Table 1). Diaspore mucilage production may be concentrated in a particular clade (or group) of plants. For example, fruits of about 60% of the 400 species of Lamiaceae in subfamily Nepetoideae produce mucilage (Ryding, 2001). Mucilage has been widely used in industry. It is added to food, cosmetics and house paint and is used to help purify drinking water, to remove solids from tannery effluent, to coat fruit for increasing shelf life, and to produce textiles and pharmaceuticals (Malviya et al., 2011). More importantly, seed coat mucilage plays many ecological roles in adaptation of plants to diverse environments.

The adaptive value of mucilage has attracted the attention of plant ecologists, and various possible functions of mucilage have been proposed in the literature. It is widely acknowledged that plant species producing mucilaginous seeds or fruits have many ecological advantages, especially under extreme desert conditions (Fahn and Werker, 1972; Evenari et al., 1982; Gutterman et al., 1967, 1969, 1973; Witztum et al., 1969; Gutterman, 1990, 1993, 1994; Gutterman and Shem-Tov, 1996). Although seed mucilage is not a universal characteristic of weeds, several important weed species (cosmopolitan weeds, noxious weeds, high abundance weeds and weeds adapted to poor soil) have mucilage (Young and Evans, 1973). These findings suggest that seed mucilage confers a considerable ecological advantage to species that colonize disturbed habitats. Further, the mucilagenous compound viscin aids in adherence of seeds of parasitic plants to the surface of the host (Gedalovich et al., 1988; Mayer, 2006). A frequently discussed ecological adaptation of seed mucilage is facilitation for imbibition of water and maintenance of moisture for plants that grow in conditions of water deficiency in arid and semiarid environments (Korobkov, 1973; Young and Martens, 1991; Huang and Gutterman, 1999a; Huang et al., 2000). Seed mucilage can also delay germination by impeding diffusion of oxygen, aid fruit and seed dispersal and defend against pathogens (Fahn and Werker, 1972; Korobkov, 1973; Young and Evans, 1973; Young and Martens, 1991; Huang and Gutterman, 1999a,b; Huang et al., 2000, 2004; Kreitschitza and Vallés, 2007).

The ecological functions of seed mucilage can vary with time. Fahn and Werker (1972) suggested that the mucilage of seeds of the cycad Ceratozamia protected them from microorganisms, insects and other consumers before dispersal. However, at dispersal the mucilage has a low tendency to be exuded, which favors dispersal by animals. Meanwhile, the sarcotesta loses its starch, becomes translucent and sticky and emits a fermentation odor.

Research has contributed substantially to our understanding of the structure, development and ecological functions of seed coat mucilage. The chemical structure, cell biology and genetics of seed mucilage production have been recently reviewed by Western (2012), who also discussed some aspects of the ecological significance of seed mucilage in germination and dispersal. In this article, we (1) synthesize (in more breadth and detail than Western (2012)) the ecological significance of mucilage in seed dispersal and germination; (2) review the role of mucilage in seed maturation, seed dormancy, seed bank maintenance and seedling growth; (3) present an extensive list of seed-mucilage producing taxa; and (4), for the first time, elaborate on the evolutionary relationships of these taxa by mapping the families onto an ordinal phylogenetic diagram. In addition, we review current knowledge about, and the progress made in, understanding the ecological functions of seed mucilage in critical stages (seed and seedling) of the plant life cycle and attempt to identify areas that remain poorly studied.

Seed maturation

Mucilage is a pectinaceous polysaccharide that may have roles in, and provide a suitable environment for, seed development in the fruit. Garwood (1985) suggested that the moist environment within the fruit may be necessary to maintain metabolic activity in the recalcitrant, mucilaginous seeds of Cavanillesia platanifolia, thus permitting seeds to maintain a sufficient level of hydration in different stages of development and keeping them in a state of readiness to germinate until the rainy season. Usadel et al. (2004) also stated that oligosaccharides of mucilage have an impact on seed development. Thus, mucilage may provide the seed with nutrients and/or a hydrated microenvironment during its development.

Despite proposed roles of mucilage in seed development, up to now the experimental evidence is extremely scarce. The reasons might be: (1) since synthesis of seed mucilage polysaccharide occurs at the same time as seed development, it is difficult to dissect (isolate) the role of seed mucilage in seed development; and (2) methods for determination of the environmental benefit of mucilage within a seed or fruit are limited. Methodological constraints have limited our understanding of the ecological role of mucilage in seed development. However, applying additional methods, such as cryo-scanning electron microscopy (CSEM), by which *in situ* development of mucilage and other seed tissues can be observed, will help us acquire a more complete picture of the role of seed mucilage. Mutants with modified mucilage production also could be useful in dissecting the role of mucilage in seed maturation.

Seed dispersal

Effective seed dispersal is a key attribute that ensures the success of a plant species. The ecological adaptive value of seed mucilage to dispersal is probably the most broadly discussed aspect of mucilage in the literature. When wetted, the mucilaginous seed coat can fix the diaspore to the soil surface and thereby influence seed dispersal. Seed mucilage of some common annuals of the Negev Desert (e.g. *Plantago coronopus* and *Anastatica hierochuntica*) adheres to the soil surface, which deters seed collection by ants and thus allows the seeds to germinate before ants collect them (Gutterman and Shem-Tov, 1997a). Lu et al. (2010) showed that seeds from the upper dehiscent fruits of the fruit/seed heteromorphic species *Diptychocarpus strictus*, which have a thick mucilage layer, adhered to soil particles much better than those from the lower indehiscent fruits, which have a thin mucilage layer, or than those of both types of seeds from which mucilage had been removed. The more mucilage the seed had, the more sand particles that adhered to the seed.

The function of seed mucilage in dispersal is closely related to its chemical heterogeneity. Seed mucilage consists of pectins and cellulose, among which the cellulose threads can strengthen anchorage. For example, achene mucilage of *Neopallasia pectinata* is rich in cellulose threads, and the extremely long mucilage threads of *N. pectinata* protect the achene against wind dispersal (Kreitschitza and Vallés, 2007). Nevertheless, quantitative evidence for this ecological role is lacking.

Topochory

Seed mucilage can absorb a large amount of water within a short period of time, which allows strong adherence of seeds to soil particles. Such an anchorage of seeds near the mother plant is very common in desert plants, because the great increase in mass of these seeds prevents them from being further dispersed by wind from favorable microhabitats (Fahn and Werker, 1972; Evenari et al., 1982; Gutterman, 1990, 1993; Huang et al., 2000). For example, seeds of *Carrichtera annua* and *A. hierochuntica* adhere to the soil surface by means of mucilage after they are dispersed and wetted (Gutterman and Shem-Tov, 1997b).

Antitelechory

Anchoring by seed mucilage is a common dispersal mechanism (or a common mechanism that prevents dispersal) of desert and Mediterranean plants (Gutterman, 1993). Long-range dispersal represents a low benefit as an adaptive trait in desert species because the most favorable environment is usually located in the vicinity of mother plants (Ellner and Shmida, 1981, 1984). For example, the thick mucilaginous coat of *P. coronopus* seeds forms an antitelechory system (adaptation that hampers dispersal) that firmly anchors seeds to the soil around the mother plant. Anchorage makes seed germination and seedling establishment dependent on the moisture and other soil resources available in that habitat, and thus it plays a central role in completion of the life cycle of plants in dry soils with scarce resources (Gutterman and Shem-Tov, 1996; Braza et al., 2010). Furthermore, production of mucilaginous seeds is one of the most effective traits enabling plants to become established on crusted soils because mucilage minimizes depletion of the local seed bank by runoff of water and provides a humid environment during germination (Gutterman et al., 1967; Gutterman and Shem-Tov, 1996, 1997b; Chambers et al., 1991; Zaady et al., 1997). Thus, proximity to a seed source has been proposed to be the most relevant predictor of emergence on soil crusts, as shown in *Helianthemum squamatum* (Escudero et al., 1999). Mucilage results not only in seed retention in a habitat but also in redistribution of seeds along vertical soil layers. In a restoration experiment, Chambers (2000) found that the density of the mucilaginous seeds of *Linum lewisii* was higher in straw mulch than in the soil under the mulch. It also has been shown that the susceptibility of a seed to removal by water erosion can be modified by the ability of the seed to produce mucilage in contact with water and that this mechanism hinders seed removal from soil by the erosion and thus enables plant succession on semi-arid Mediterranean slopes (Ellner and Shmida, 1981; García-Fayos et al., 2010).

Epizoochory

Seed mucilage can also enhance epizoochory by increasing the ability of diaspores to adhere to animals. Salisbury (1961) observed that mucilaginous seeds became attached to the feathers of birds when feeding in ruderal communities and thus were transported to new areas, where they were removed during preening. Additionally, Nunez et al. (2008) found that the triglyceride-rich fruits of *Coussapoa asperifolia* subsp. *magnifolia* seem to be excellent for sealing of nests of the stingless bee (*Melipona* sp.) in the hot and humid Amazonian climate, in which otherwise water may enter in the crevices and damage cells, provisions and brood (Roubik, 1989). Therefore, the authors reasoned that this bee is the primary (and perhaps sole) disperser of *C. asperifolia* subsp. *magnifolia* seeds.

Endozoochory

It has been suggested that many animals feed on seeds or fruits that have mucilage, thereby providing efficient dissemination over a large area for these species. Savage et al. (1969) observed that chukar partridges (*Alectoris gracea*) prefer the mucilaginous seeds of yellowflower pepperweed (*Lepidium perfoliatum*), tumblemustard (*Sisymbrium altissimum*) and tansymustard (*Descurainia pinnata*) over downy brome (*Bromus tectorum*) caryopses, which formed the bulk of their diet during feeding trials. However, Lobova et al. (2003) suggested that mucilage of *Cecropia* fruits is not nutritionally important to bats, since the mucilaginous cells often are intact after passing through the bat's intestines, whereas the perianth surrounding the fruit is completely digested. They suggested that mucilage covering the fruit provides lubrication for fruit passage through the digestive tracts of animals. Additionally, no decrease in seed survival was reported after the mucilaginous seeds passed through animal's intestines. Nunez et al. (2008) also showed that the mucilaginous fruits of *C. asperifolia* subsp. *magnifolia* are unpalatable to monkeys and birds, because they have high levels of triglycerides but very low levels of sugar (α- and β- glucose). In these cases, it seems that the main benefit of seed mucilage is to offer protection for the seed in a hostile environment and thus to improve its survival.

Passage of diaspores through the intestines of animals removes mechanical and chemical barriers from the diaspores (Traveset and Verdú, 2002), which would subsequently affect the germination of mucilaginous seeds. For example, after passage through the digestive tracts of animals seeds of *Cecropia obtusifolia* germinated to higher percentages than those not consumed by animals (Estrada et al., 1984; Estrada and Coates-Estrada, 1986). Fleming (1988) found similar results for *C. peltata*. In addition, fruit passage through the animal's digestive tract increases seed survival by removing the perianth and some of the mucilaginous tissue from the fruits, thereby influencing seed germination (Gutterman et al., 1973; Lobova et al., 2003). The mucilage prevents germination until birds eat the diaspores and removes the mucilage, thus permitting the seeds to germinate (Baskin and Baskin, 1998). In contrast, Vázquez-Yanes and Orozco-Segovia (1986) concluded that passage of seeds of *C. obtusifolia* through the digestive tracts of bats did not influence germination. In these studies, mucilage was removed when the seeds passed through the digestive tract. Lobova et al. (2003) also suggested that external mucilage production does not play a significant role in the germination of *Cecropia* seeds, since they germinate with or without mucilage in nature and in the laboratory. The benefit of mucilage in endozoochory is currently under debate, probably because this effect varies with the plant species and with the animals that eat the seed.

Hydrochory

The mucilage layer can reduce the specific weight of diaspores of some species, thus facilitating their floatation on still or moving water (Fahn and Werker, 1972; Young and Evans, 1973; Boeken and Shachak, 1994; Huang et al., 2000), as in *Blepharis* spp. (Gutterman et al., 1967, 1969; Witztum et al., 1969; Gutterman, 1993), *A. hierochuntica* (Friedman and Stein, 1980; Gutterman and Shem-Tov, 1997a), *Reboudia pinnata*, *C. annua* (Evenari and Gutterman, 1976) and *P. coronopus* subsp. *commutata* var. *crassipes* (Gutterman and Shem-Tov, 1996, 1997a). In a few cases, however, diaspores with only a little or no mucilage float better than those with lots of mucilage. In the seed-heteromorphic species *P. coronopus* forma *pygmaea*, a fully developed fruit may contain four large nonmucilaginous basal seeds and one small mucilaginous apical seed. The small apical seed with a narrow mucilage sheath floated better than

the large basal seeds with a wide mucilage sheath (Dowling, 1933). In *Artemisia monosperma*, achenes from which the mucilage had been removed floated for a longer period of time than those with mucilage left intact (Huang and Gutterman, 1999a). Thus, the effect of mucilage on seed floatation may depend on the relative specific weight of seed to mucilage, i.e. if the specific weight of seeds is higher than that of mucilage, the presence of mucilage would aid seed floatation and vice versa.

In the Negev Desert, *A. hierochuntica* seeds float on runoff water and are dispersed along runnels on slopes and in the runoff streams (Friedman and Orshan, 1975; Friedman and Stein, 1980; Friedman et al., 1981; Gutterman and Shem-Tov, 1997b). For species growing on a riverside, such as *Artemisia dracunculus*, the presence of seed mucilage also may play an important role in dispersal (Kreitschitza and Vallés, 2007). The mucilaginous seed coat is also suggested to be vital for spreading of *Brassica tournefortii* along shorelines, and it sticks to tires, shoes, boats and the plant itself, thereby aiding the dispersal of *B. tournefortii* across Lake Mead, southern Nevada (Bangle et al., 2008).

Soil seed bank maintenance

Seed banks are ecologically important components of population and vegetation dynamics that affect both ecosystem resistance and resilience. Seed mucilage plays an important role in maintaining a soil seed bank, especially for desert plants. Mucilage of *Dillenia indica* keeps recalcitrant seeds glued to the inside of the large fruit, thus preventing them from drying during the long dry season before the monsoon and from escaping the fruit and being eaten (Thapliyal et al., 2008). Gutterman and Shem-Tov (1997b) suggested that seed mucilage may be important for the initiation of the repair mechanisms within the seed. Two of our recent reports have shown that when seeds of the desert plant *Artemisia sphaerocephala* are hydrated via desert dew, seed mucilage facilitates DNA repair (Huang et al., 2008; Yang et al., 2011). This repair mechanism subsequently helps the seeds of this species to retain viability, thus maintaining a functional soil seed bank in the harsh desert environment (Yang et al., 2011).

Seed dormancy

Seed dormancy is an important trait that results from a block to germination when environmental conditions such as light, moisture and temperature are suitable (Baskin and Baskin, 1998, 2004). Fresh seeds of *Arabidopsis thaliana* are dormant and thus have a low germination percentage. The effect of seed mucilage on seed dormancy of this species has been investigated genetically. Léon-Kloosterziel et al. (1994) showed that two mutants, *transparent testa glabra1* (*ttg1*) and *aberrant testa shape* (*ats*), lacking seed coat mucilage have reduced dormancy, and they proposed that the reduced dormancy may be due to increased oxygen diffusion in the absence of seed coat mucilage since dormancy could be broken by pricking the seed coat of wild type seeds. Germination of *Blepharis persica* seeds is also stimulated by removing the mucilage or the seed coat and by increasing the percentage of oxygen to which they are exposed (Witztum et al., 1969). However, Debeaujon et al. (2000) reported that *A. thaliana glabra2* (*gl2*) seeds, which also lack seed coat mucilage, have normal seed dormancy. They suggested that factors other than the absence of seed coat mucilage are responsible for the observed loss of seed dormancy in *ttg1* and *ats*. The reduced seed dormancy may be caused by the absence of tannins in the seed coat of *ttg1* mutants and in the aberrant seed coat of *ats* mutants (Debeaujon et al., 2000). This genetic analysis also showed that seeds of

the three mutants *ats*, *gl2* and *ttg1* have reduced seed longevity in comparison to wild type seed lots after storage for 4 years at room temperature (Debeaujon et al., 2000). Recently, Toorop et al. (2012) reported that mucilaginous seeds in twelve genotypes of shepherd's purse (*Capsella bursa-pastoris*) all showed stronger secondary dormancy than non-mucilaginous seeds. Meanwhile, non-mucilaginous seeds had lower mass but higher nitrogen than mucilaginous seeds; thus, whether the stronger secondary dormancy of mucilaginous seeds was due to the mucilage or resources in the seed is unknown.

Seed germination

Seed mucilage has long been proposed to promote seed germination through attraction and retention of water surrounding the seed (Harper and Benton, 1966; Fahn and Werker, 1972; Young and Martens, 1991; Huang et al., 2000; Penfield et al., 2001). Seed mucilage enhances water uptake during germination due to its hygroscopic properties (Swarbrick, 1971; Garwood, 1985). Further, mucilaginous seeds on the soil surface have better contact with the soil particles, and therefore their water absorption is much better than that of non-mucilaginous seeds (Hadas, 1982; Gutterman and Shem-Tov, 1997a). Mott (1974) found that mucilage aids seed hydration and germination of three species from an arid region of Western Australia, *Helipterum craspedioides*, *Helichrysum cassinianum* and *Aristida contorta*, in the presence of some surface water. Baiges et al. (1991) suggested that seed mucilage in the dispersal units (seeds or fruits) of *Euphorbia* species helps create appropriate conditions for establishment and germination. We recently showed that seed mucilage in *A. sphaerocephala* aids germination in osmotically and saline-stressful habitats of the cold desert environment in northwestern China (Yang et al., 2010). Presence of mucilage on seeds of *Alyssum minus* during imbibition significantly increased germination percentages under increased water stress (Sun et al., 2012).

However, seed mucilage can also act as a physical barrier for regulating diffusion of water and oxygen to the inner tissue of the seed and thereby prevent germination under unsuitable conditions (Gill, 1935; Gutterman et al., 1967, 1973; Witztum et al., 1969; Fahn and Werker, 1972; Grubert, 1974, 1981; Panigrahi, 1986; Gutterman and Shem-Tov, 1996; Werker, 1997). Witztum et al. (1969) speculated that the physical barrier of mucilaginous seed coats plays an ecological role in prevention of germination of *B. persica* seeds in nature when conditions are unsuitable for seedling establishment. Chemicals in seed mucilage may directly regulate germination. Both inhibiting and promoting effects of seed mucilage have been reported for seeds of several species (Garwood, 1985; Figueiredo, 1986). However, more evidence is needed for the chemical regulation of mucilage on the seed germination. In addition, it remains unknown which compound(s) is(are) responsible for the chemical effect and whether such effect is context-dependent (i.e. variation in different habitat or life stage).

Genetic analyses have also been conducted to explain the mechanism of seed mucilage in regulating germination. Although *Arabidopsis* seed mucilage mutants *ttg1-1* and *gl2-1* germinate normally under standard laboratory conditions, they have a decreased ability to do so when exposed to osmotic stress compared with that of the wild type (Penfield et al., 2001). A similar reduction in germination under limited water supply has been found for a mutant for the gene *Atsbt1.7* (Rautengarten et al., 2008). The *defective in cuticular ridge1* (*dcr-1*) mutant seeds, which are defective in mucilage extrusion, also exhibit significantly lower germination percentage than wild-type seeds under water-limiting

conditions (Panikashvili et al., 2009). Moreover, Arsovski et al. (2009) reported that not only *mucilage-modified4-1* (*mum4-1*) but also double mutants of *myb61 mum4*, *mum2 mum4* and *mum enhancers/mucilage-modified4* (*men mum4*) have delayed germination compared with wild-type seeds. These findings suggest that both mucilage quantity and properties are important for efficient seed hydration and germination, even under moist conditions (Arsovski et al., 2009).

Seedling growth

The seedling is the critical stage in the plant life cycle, and seed mucilage plays a role in regulating its development. First of all, the sticky nature of seed mucilage may anchor the seed to the soil surface and thus help the seedling by lubricating the radicle as it penetrates the soil (Schat, 1981; Lobova et al., 2003). Removal of the seed mucilage from *A. monosperma* seeds before germination may affect seedling development and causes a decrease in their size (Huang and Gutterman, 1999a,b; Huang et al., 2000). Yokotani-Tomita et al. (1998) speculated that rhamnose-containing oligosaccharides exuded from germinating seeds have a role in hypocotyl growth. Such an effect could also be due to sugars such as fructose in the seed mucilage (Usadel et al., 2004).

Shoot growth of several plant species is significantly promoted when they are cultured together with cress (*Lepidium sativum*) seeds, but root growth is inhibited. In contrast, growth of cress seedlings is not influenced by cress seeds (Hasegawa et al., 1992a). Interestingly, this effect is not caused by contact with cress seeds but is due to the mucilage of the germinated cress seeds (Hasegawa et al., 1992a). Longman and Callow (1987) and Ray et al. (1988) further reported that the mucilage of germinated cress seeds containing polysaccharides reduced binding of the fungus *Pythium aphanidermatum* to cress roots, which led to the observed effect. In a subsequent study, the allelopathic substance was identified as lepidimoide (sodium 2-O-rhamnopyranosyl-4-deoxy-threo-hex-4- enopyranosiduronate) (Hasegawa et al., 1992b).

The role of seed mucilage in seedling growth also has been studied micrographically. It has been reported that mucilage from other plant tissues can also play roles in the regulation of seedling growth. Kawasaki et al. (2001) observed that mucilage in mucilage ducts in the corm of *Colocasia esculenta* started to decompose and decrease in density from the proximal to the distal part and also from the periphery to the center of the duct. Thus, this observation provides direct evidence that both starch mobilization and mucilage mobilization function to supply the substances necessary for sprouting and regeneration of the plant body at least during the first half of the vegetative stage (Kawasaki et al., 2001).

In an ecological context, the degradation of seed mucilage by soil microfloras also may promote seedling growth. Recently, we showed that the biodegradation of seed mucilage of the cold desert shrub *A. sphaerocephala* is a very complicated process. Thus, mucilage can be biodegraded either to CO_2 or to small molecules (e.g. sugar), and an increase in soil microbial biomass occurs during biodegradation. The biodegradation also promotes early seedling growth in barren sand dunes, which is associated with a large soil microbial community that supplies substances promoting seedling establishment (Yang et al., 2012b). However, it is unclear whether the promotion effect is caused by absorption of breakdown products by the seedling, exudates of soil microbe metabolism or both. Thus, concrete interactions between the seed mucilage and soil microbes in promotion of seedling growth remain to be demonstrated.

Adaptation and evolutionary aspects

The mucilage layer on the seed coat is not homogenous, and different layers within the mucilage may differ in their ecological functions. *A. thaliana* seed mucilage consists of two layers that differ in composition and structure, implying that they may be functionally different (Macquet et al., 2007a,b). Since pectins are known to be degraded by bacterial and fungal enzymes (Willats et al., 2001), the water-soluble outer mucilage may allow mucilage protrusion around the seed and thereby stimulate or inhibit the growth of bacteria and fungi and enhance the rhizosphere for seedling growth (Macquet et al., 2007b). In contrast, adhesive qualities and tight linkage of the inner layer of mucilage to the seed coat possibly have a role in seed dispersal, anchorage of seed to soil particles and/or the control of germination.

Furthermore, ecological functions of seed mucilage change not only spatially (i.e. different layers) but also temporally. Gutterman and Shem-Tov (1997b) argued that the ecological significance of mucilage of plants in the Negev Desert differed in winter and summer. In winter, the main function is seed water retention and seed-soil particle contact when seed dispersal occurs, while in summer dew absorbed by seed mucilage may allow DNA repair mechanisms and priming for the germination process when it is the season for seed germination.

Production of seed mucilage is an ecologically important trait that facilitates successful establishment of plants in diverse habitats, and thus it may be an adaptation to arid, ruderal and disturbed environments. The adaptive benefit of seed mucilage production has been confirmed for *A. annua* and *A. biennis* in disturbed areas, *N. pectinata* in semiarid areas (Cullen, 1975; Polyakov, 1995; Kreitschitza and Vallés, 2007) and *Lepidium flavum*, *L. nitidum*, *Plantago lanceolata*, *Cardaria draba* and *A. thaliana* in ruderal habitats (Young and Evans, 1973; Western et al., 2000).

Since seed mucilage facilitates plant establishment in a wide range of habitats, it would not be surprising if habitat diversity among seed-mucilaginous species is, at least in part, due to differences in amount of mucilage. Achene mucilage of plants of some *Artemisia* and *Neopallasia* taxa that occur in dry habitats (e.g. *A. barrelieri* and *A. annua*) are characterized by a large amount of mucilage and by fast development of a mucilage envelope. In subfamily Nepetoideae (Lamiaceae), species that grow in dry habitats are more often myxodiasporic than species that grow in moist or damp habitats (Ryding, 1992, 2001). However, some populations of polyploid species (*A. campestris* and *A. campestris* ssp. *sericea*) and diploid species (*A. verlotiorum* and *A. vulgaris*) that occur in relatively fertile and moist habitats do not produce seed mucilage (Kreitschitza and Vallés, 2007). These results suggest that habitat diversity may select for differences in the amount of seed mucilage, but these correlations need to be confirmed.

Kulich et al. (2010) reported significant differences between the amount of mucilage on seed coats of seeds produced on primary and secondary infructescences of *A. thaliana*. Because *A. thaliana* is an opportunistic ruderal species, the authors proposed that it may be advantageous for it to produce the first seeds as quickly as possible (i.e. less mucilage with a smaller energy investment) and thus generate at least some progeny. However, later, after accumulation of more biomass it may be advantageous for the plant to produce higher quality seeds surrounded by more mucilage that increases tolerance to transient water deficit during germination. This strategy may contribute to broadening the available ecological niche for *A. thaliana* (Kulich et al., 2010). These studies provide preliminary evidence for the adaptive values of seed mucilage.

Ordinal phylogenetic position of plant families that include species with seed coat mucilage based on available data shows that seed mucilage is mainly found in phylogenetically advanced
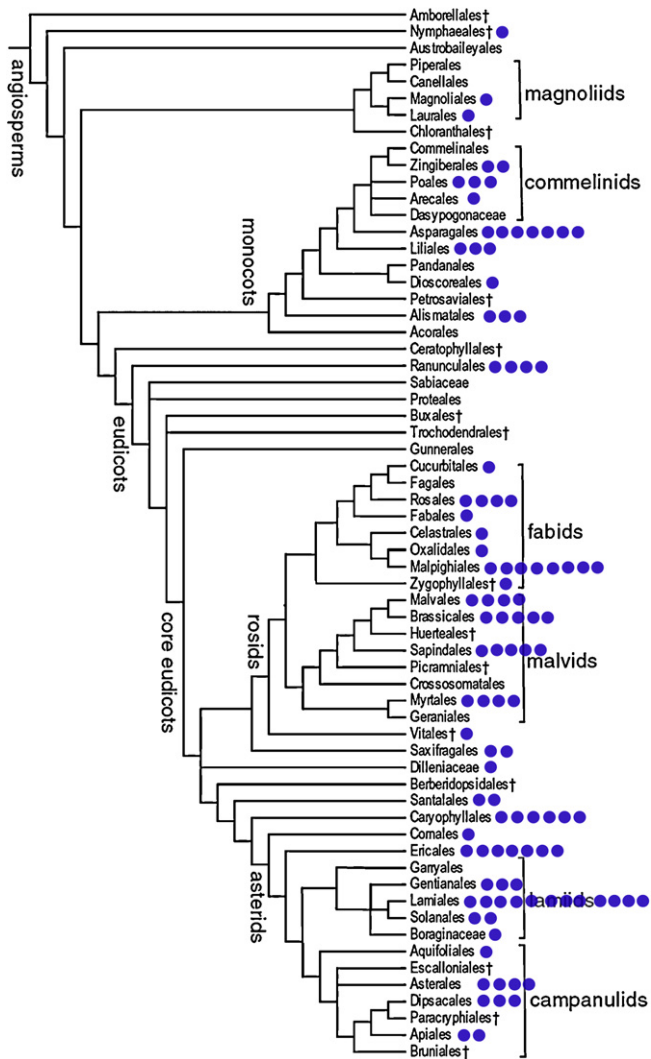
Fig. 1. Ordinal phylogenetic position of plant species with seed coat mucilage in angiosperms. Each filled circle represents a family in which seed mucilage has been documented. The phylogenetic diagram is from the Angiosperm Phylogeny Group (2009).

families (Fig. 1). Only three families (2.7%) that produce seed mucilage are in magnoliids and Nymphaeales, and 18.2% of the families that produce seed mucilage are monocots. In contrast, most taxa (79.1% of families) that have seed mucilage are in the eudicots, especially in rosids and asterids. It is noteworthy that species producing seed mucilage are found in the two most species-rich and geographically widely distributed families Poaceae and Asteraceae. These two families alone contain >30,000 species or >10% of the extant angiosperms (Thorne, 2000; Mabberley, 2008). At present, 17 genera of Asteraceae and 2 genera of Poaceae have been reported to have mucilaginous seeds (Supplementary Table 1); however, many species in these families need to be investigated to determine if they can produce mucilage. In gymnosperms, seed mucilage seems to have been reported only for *Ceratozamia* in the family Zamiaceae (Fahn and Werker, 1972). Further inspection of phylogenetic position of plant families that include species with seed coat mucilage indicates a possible phylogenetic advantage of mucilage, because more highly advanced families with mucilage production have members growing in dry habitats (e.g. Asteraceae, Brassicaceae and Poaceae) than basal taxa (e.g. Nymphaeales and Magnolids in moist habitats). However, if a trait such as mucilage

production is phylogenetically independent families with the most taxa (e.g. Rosids) will have a high number (by chance) of mucilage-producing taxa compared with basal families with a low number of taxa (e.g. Nymphaeales). The origin of seed mucilage appears to extend at least as far back in geological history as the Middle Eocene (Smith and Stockey, 2003). Smith and Stockey (2003) identified "a probable zone of mucilage" in seeds of the extinct Araceae species *Keratosperma allenbyense* from the Middle Eocene Princeton Group, Allenby Formation (48.7 Ma). Our preliminary analysis may suggest that seed mucilage is an evolutionarily advanced trait. However, the evolutionary aspect of seed mucilage probably is far more complicated than we currently think.

Concluding remarks and future prospects

It appears that seed mucilage is important for seed-mucilage producing plants to successfully complete the critical stages of their life cycle in a wide range of environments, especially in stressful ones. Based on the current understanding of the ecological function of seed mucilage, we present a conceptual model to summarize the roles of mucilage in seed maturation, seed dispersal, soil seed bank maintenance, seed dormancy, seed germination and seedling growth (Fig. 2).

The production of mucilage during seed development is a significant metabolic investment, and yet its potential physiological and ecological roles remain an enigma (Western et al., 2000; Macquet et al., 2007a,b). In particular, the functions of mucilage in the diversity of habitats in which seed-mucilage producing species occur are still not clear (Huang et al., 2011). Therefore, we might be at the threshold of understanding the ecological functions that seed mucilage plays in the plant life cycle. First of all, several important aspects of the ecological functions of seed mucilage have been overlooked. Thus far, most studies have focused on its role in seed dispersal and germination. Roles of mucilage in seed maturation, soil seed bank maintenance, seed dormancy and seedling growth remain to be addressed.

Secondly, there are few species (e.g. *A. thaliana* and a few *Artemisia* taxa) that have been used in studies of the ecological function of seed mucilage. Many plant taxa are known to produce seed mucilage, and thus it is uncertain whether the conclusions drawn from studies on a few taxa can be generalized. Further studies using more species could answer this question and possibly define new functions for seed mucilage. Thirdly, current studies on the ecological importance of seed mucilage largely have been conducted in arid environments. In addition to plants inhabiting arid areas, some plants occurring in other environments (e.g. humid and disturbed habitats) also produce seed mucilage. At present, how seed mucilage influences the life cycle of such plants is unclear. Fourthly, the primarily direct ecological observations widely used in most studies have resulted in a hypothetical knowledge of the functions of seed mucilage. It is necessary to combine additional physiological, genetic and proteomic tools (e.g. expression profiling technology and immunohistochemistry) to explain the mechanisms underlying the ecological functions of seed mucilage. Fifthly, more attention should be paid to the evolution and phylogeny of plants that produce seed mucilage. Given the large number of plants with a mucilaginous seed coat, processes that occur in a diversity of habitats and taxa would provide valuable information to understand the ecological functions from evolutionary and phylogenetic perspectives. Further investigations of more species that occur in diverse habitats using molecular and proteomic approaches might reveal additional adaptive and evolutionary advantages of seed mucilage.
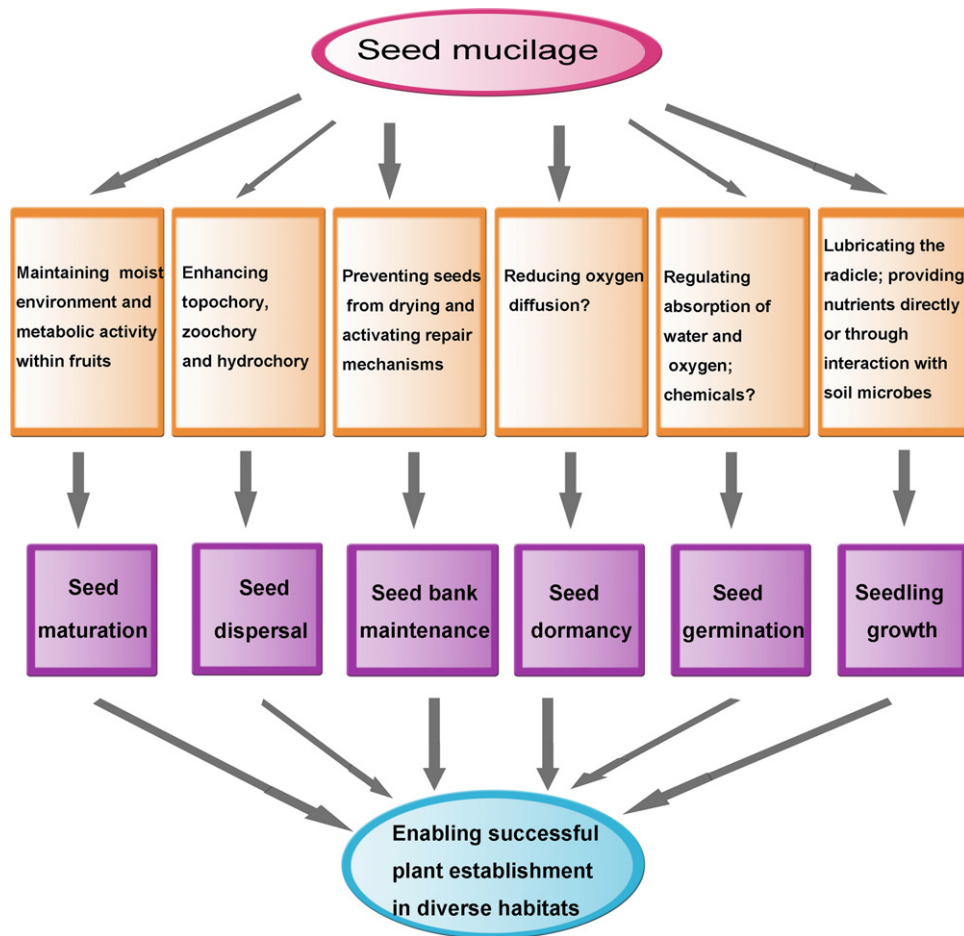
Fig. 2. A conceptual model for ecological roles of seed mucilage in the critical stages of the plant life cycle.

Finally, our recent publications revealed the enhancement of seedling emergence by seed mucilage in a sandy desert environment (Yang et al., 2012a) and highlighted the ecological function of mucilage degradation, notably the interaction between mucilage degradation and soil microfloras (Yang et al., 2012b). This indicates that the ecological importance of seed mucilage is not limited to the seed *per se* but that it also plays a role in the regulation of soil biological processes. Therefore, dissection of the seed mucilage regulatory mechanism will be required to reveal how the network of interactions of seed mucilage regulates the soil microbial community that interacts with seed germination and seedling growth.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2012.09.002.

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