The evolution of seeds

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Summary

The evolution of the seed represents a remarkable life-history transition for photosynthetic organisms. Here, we review the recent literature and historical understanding of how and why seeds evolved. Answering the 'how' question involves a detailed understanding of the developmental morphology and anatomy of seeds, as well as the genetic programs that determine seed size. We complement this with a special emphasis on the evolution of dormancy, the characteristic of seeds that allows for long 'distance' time travel. Answering the 'why' question involves proposed hypotheses of how natural selection has operated to favor the seed life-history phenomenon. The recent flurry of research describing the comparative biology of seeds is discussed. The review will be divided into sections dealing with: (1) the development and anatomy of seeds; (2) the endosperm; (3) dormancy; (4) early seed-like structures and the transition to seeds; and (5) the evolution of seed size (mass). In many cases, a special distinction is made between angiosperm and gymnosperm seeds. Finally, we make some recommendations for future research in seed biology.

Think of the fierce energy concentrated in an acorn! You bury it in the ground, and it explodes into an oak! Bury a sheep, and nothing happens but decay.

George Bernard Shaw

I. Introduction

The seed habit is the most complex and successful method of sexual reproduction in vascular plants. The seed plants (*Spermatophyta*) comprise two major groups: the *Acrogymnospermae* (also referred to as gymnosperms; *c.* 800 living species) and the *Angiospermae* (also referred to as angiosperms; *c.* 250 000 living species) (Cantino *et al.*, 2007). These groups are by far the most diverse lineages within the vascular plants. Charles Darwin described the rapid rise and early diversification within the angiosperms during the Cretaceous as 'an abominable mystery'. Although many seed plant groups are known from the fossil record, only five lineages are extant (Fig. 1a): angiosperms and four gymnosperm groups (conifers, cycads, ginkgos, Gnetales). The classical 'anthophyte hypothesis' (based on the flower-like reproductive structures of the different clades), that is, that the angiosperms and the Gnetales are closely related and form a clade, was rejected (reviewed by Doyle, 2006). All molecular and morphological analyses support angiosperm monophyly (Frohlich & Chase, 2007; Soltis *et al.*, 2008; Pennisi, 2009). Molecular phylogenetic analyses of seed plants now indicate that the living gymnosperm groups are monophyletic, with Gnetales related to conifers (Doyle, 2006; Hajibabaei *et al.*, 2006; Frohlich & Chase, 2007). Frohlich & Chase (2007) state that paleobotanists are increasingly willing to consider extant gymnosperm monophyly, but with varying degrees of surprise and disquiet over the implications. Based on these molecular analyses, no other living gymnosperm group is directly related to the angiosperms. Morphological analyses of extinct and extant gymnosperms using critically revised data sets suggest that this molecular arrangement should be accepted (reviewed by Doyle, 2006). When living and fossil taxa are considered together and constrained into the molecular topology, the combined analysis reveals a revised 'anthophyte clade' consisting of the extinct gymnosperm groups, glossopterids, *Pentoxylon*, Bennettitales, and *Caytonia* as sister to angiosperms (Fig. 1a; Doyle, 2006; Frohlich & Chase, 2007; Soltis *et al.*, 2008). The monophyly of the extant gymnosperms places them all equally distant from the angiosperms, which means that the lineage that eventually produced angiosperms derived from a common ancestor with extant gymnosperms much earlier than previously thought, that is, from among the paraphyletic seed ferns (Fig. 1a). In the present article we use this as the phylogenetic framework to review what is known about the evolution of the seed habit.

Fig. 1 Origin and evolution of the seed habit. (a) Seed plant phylogeny considering major extinct and extant gymnosperm and angiosperm clades. Based on molecular phylogenetic evidence, the extant gymnosperms form a monophyletic group and the extant angiosperms form a distinct monophyletic group. Note that the precise evolutionary connections between the different gymnosperm groups are unknown and that the ancestors of the angiosperms are unknown. Extinct gymnosperm groups (insets of fossil drawings and images) include the paraphyletic group of seed ferns (Lyginopteridopsida), such as Devonian–Carboniferous Lyginopterids (e.g. *Lagenostoma*, from Scott, 1909) and Carboniferous–Permian Medullosans (e.g. *Stephanospermum*, see panel b). Other groups/insets: Bennettitales (cycadeoids, from Scott, 1909; Zimmermann, 1930), Glossopteridales (glossopterids), Gigantopteridales (gigantoperids, seed-bearing leaflet from Li & Yao, 1983), Gnetopsida (gnetophytes: Ephedridae, Gnetidae, Welwitschiidae), monocots (maize grain), Caryophyllids (*Beta*; Hermann *et al.*, 2007). Timescale: geological eras, periods, time in million yr ago. (b–f) Structural biodiversity of gymnosperm and angiosperm seeds with special consideration of the covering layers. (b) *Stephanospermum akenioides* – drawing of a fossil medullosan seed fern ovule (Permian–Carboniferous Lyginopteridopsida; *c.* 1 cm long). Within the megagametophyte, archegonia with egg cells are evident. The megasporangium (nucellus) is surrounded by the integument which evolved into the three-layered testa. The micropylar extension, which in other *Stephanospermum* specimens forms an apical funnel to capture wind-blown pollen and a pollen chamber is evident. The nucellus and the megagametophyte are poorly perserved in the *Stephanospermum* ovule fossils. The megaspore membrane is robust and consists of a distinctive network of granules and rods of sporopollenin covered by a homogeneous outer layer (from Schnarf, 1937). (c) Mature seeds of extant gymnosperms (cycad and conifers). The diploid embryo is enveloped by the haploid megagametophyte and the diploid testa; remnants of the nucellus may be present. Left of panel – cycad seeds: in the cycad ovule the micropylar opening produces a liquid pollination drop, which catches wind-blown pollen and allows it to enter the pollen chamber. The pollen germinate and the pollen tubes grow into the nucellus tissue. There they release spermatozoids that swim to the archegonia and fertilize the egg cells. About half a year time difference is often found between cycad pollination and fertilization. The *Cycas* ('sago palm') embryo grows within the seed, and germination can occur only as the embryo has reached a similar size as the seed (morphological dormancy, MD). The embryo usually has two to four fleshy cotyledons, and the radicle is usually not fully developed as a distinct organ at the time of seed maturity. Seeds of tropical and subtropical *Zamia* species require many months of warm stratification before they will germinate (MPD). Right of panel – conifer seed: conifer ovules do not have pronounced pollen chambers and pollen grains do not release swimming spermazoids, but immobile sperms. The mature pine (*Pinus* spp.) seed contains an uncurved embryo with many cotyledons. The embryo is embedded in the megagametophyte tissue. The ovulate pine cone becomes woody as it matures. Seeds of *Pinus* spp. are either nondormant or have physiological dormancy (from Engler, 1926; Schnarf, 1937). (d) Mature seed of a basal angiosperm (Nymphaeaceae, water lily) with diploid endosperm and perisperm (from Kirchner *et al.*, 1938). (e) Mature seed of a basal eudicot (Ranunculaceae) with abundant triploid endosperm and tiny embryo (from Engler & Prantl, 1891). (f) Mature seeds of core eudicots that differ in endosperm abundance: astrids (tobacco), rosids (Arabidopsis).

Charles Darwin's studies of seeds have contributed to his ideas on evolution and distribution of plant species (Black, 2009). We consider the seed habit to be a preadaptation for the quick dominance of the angiosperms. In addition, the enhanced sporophyte, reduced gametophyte, and a wide range of morphological adaptations (roots, leaves, the cuticule and stomata, to name a few) allow seed plants to occur in a wide variety of habitats and dominate the terrestrial flora of earth. The seed habit itself, in addition to vegetative traits such as the production of wood by a secondary meristem (cambium), contributed decisively to the evolutionary success of the gymnosperms and angiosperms.

In this review of the evolution of the seed habit, we will start by describing seed development, including the evolution of the endosperm, and dormancy. There is a lot of terminology involved. We present this in Section II 'Seed development' and Table 1 to refresh the reader's vocabulary and to set the stage for a more complete understanding of the seed system. With this terminology introduced, we will turn our attention to the early evolution of seed-like structures and the transition to the seed habit. Finally, we will consider the range of variation in seed size (mass) and its ecological correlates by reviewing the recent flurry of research in that area.

II. Seed development

In gymnosperms and angiosperms, seeds develop from ovules (Finch-Savage & Leubner-Metzger, 2006; Frohlich & Chase, 2007). Ovules consist of a stalk that bears the nucellus (equivalent to the megasporangium; diploid maternal tissue). The nucellus is enveloped by one (gymnosperms) or two (angiosperms) covering layers (diploid maternal tissue), called the integuments. An ovule

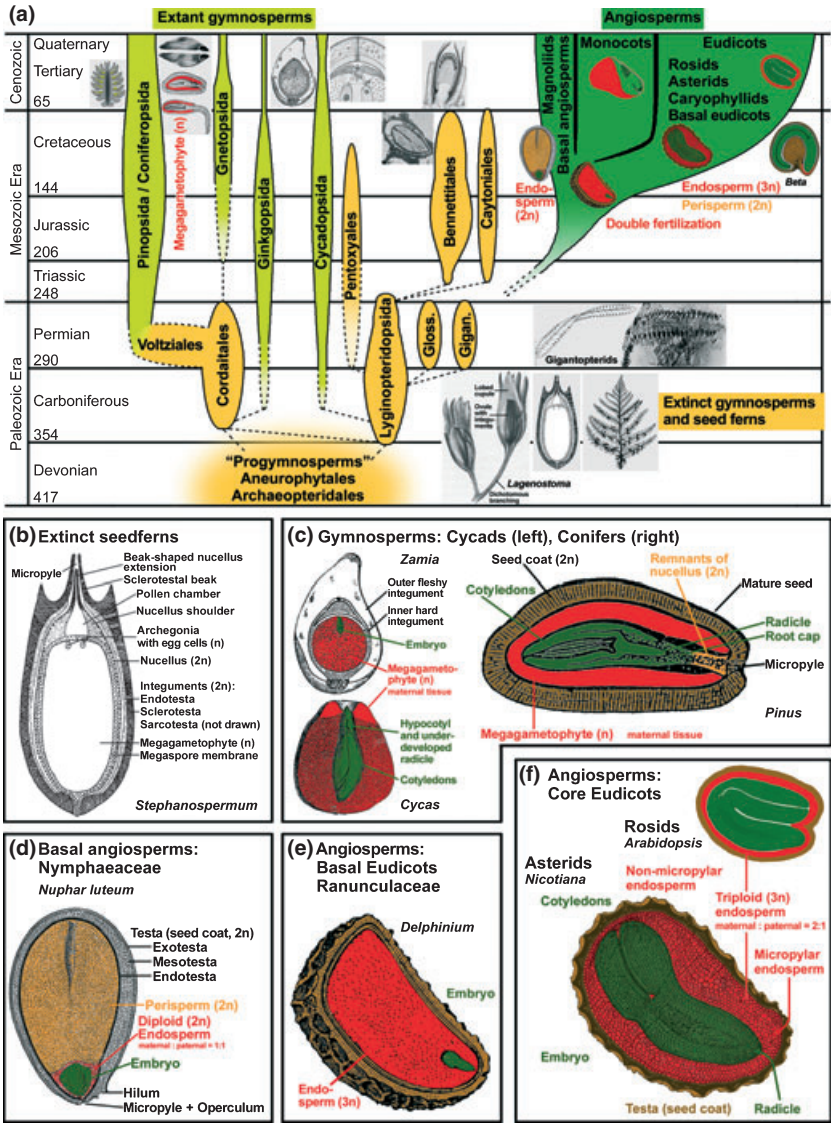

Table 1 Description of frequently used terms

Ovule	Structure that consists of the integument(s) surrounding the nucellus (megasporangium); unfertilized, immature seed precursor
Nucellus	Megasporangium; surrounds the megagametophyte; can develop into perisperm after fertilization
Megagametophyte	Female gametophyte, contains the female haploid egg cells (gametes) and several thousand (gymnosperms) or typically three to eight (angiosperms) other cells; the mature angiosperm megagametophyte is called the embryo sac
Integuments	One (gymnosperms) or two (angiosperms) outer layers of the ovule, having an apical opening (micropyle); develop after fertilization into the seed coat (testa)
Micropyle	Apical opening of the integuments; allows the pollen tube to enter the nucellus to release sperm for fertilization
Testa	Seed coat, derived from the integuments of the ovule; dead maternal tissue
Endosperm	Arises from the fusion of a second sperm nucleus with the central cell nucleus of the embryo sac during double fertilization; nutritional tissue during seed development and in the mature seed of most angiosperms, in between testa and embryo
Perisperm	Derived from the nucellus after fertilization; maternal nutritional tissue in the mature seed of some angiosperms
Ovary	Usually lower portion of the angiosperm pistil (carpel or fused carpels) containing ovules; fruits are mature ovaries; ovary tissue develops into the pericarp
Pericarp	Fruit coat of angiosperm fruits, develops from the mature ovary wall and other flower tissues; surrounds the seed(s)

is therefore, in a developmental sense, an unfertilized, immature seed precursor (Gasser *et al.*, 1998) and, in a morphological and evolutionary sense, a megasporangium surrounded by integument(s). These integument(s) develop into the testa (seed coat), of which in mature seeds the outer cell layer(s) of the outer integument usually form a dead covering layer, while inner cell layer(s) may remain alive (Bergfeld & Schopfer, 1986; Debeaujon *et al.*, 2000; Windsor *et al.*, 2000; Haughna & Chaudhuryb, 2005).

Within the nucellus, a megaspore develops into a haploid megagametophyte (female gametophyte). The megagametophytes of gymnosperms and angiosperms (Fig. 2) differ considerably (Floyd & Friedman, 2000; Baroux *et al.*, 2002). The mature gymnosperm megagametophyte is multicellular, usually several archegonia develop within the megagametophyte and one egg forms in each archegonium (Fig. 2b, left image). In most angiosperm species, the megagametophyte, in its mature state also called the embryo sac, is seven-celled and eight-nucleate, referred to as the Polygonum-type (Fig. 2b, right image) (Floyd & Friedman, 2000; Baroux *et al.*, 2002; Friedman & Williams, 2004; Berger *et al.*, 2008; Friedman & Ryderson, 2009). Less frequently the mature megagametophyte is four-celled and four-nucleate, called the Nuphar/Schisandra-type, which can be found in the basal angiosperms, namely Nymphaeales and Austrobaileyales (Fig. 2b, middle). This is thought to be the ancient type of embryo sac (Floyd & Friedman, 2000; Baroux *et al.*, 2002; Friedman & Williams, 2004; Berger *et al.*, 2008; Friedman & Ryderson, 2009).

After pollination, in all extant angiosperms and most gymnosperms a pollen tube is formed, through which the nonmotile sperm reaches and fertilizes the egg cell, which leads to development of the diploid embryo (Fig. 2b). This siphonogamic type of sperm transfer is typical for all extant seed plants, with the exception of cycads and ginkgo, which have multiflagellated, swimming sperm that are released from the bursting pollen grain in the vicinity of the archegonium. Fossil and living taxa suggest that siphonogamy arose independently in conifers and on the line leading to the angiosperms (Fig. 15 in Doyle, 2006).

A typical mature embryo is differentiated and exhibits developmental polarity that is divided into the radicle (embryonic root) and the shoot with the cotyledon(s) (embryonic leaves) (Fig. 1c–f). The gymnosperms have naked seeds; their seeds are not enclosed by an ovary and are usually found naked on the scales of a cone. In a typical mature gymnosperm seed, the embryo has two covering layers: the haploid maternal megagametophyte with stored nutrients and the diploid integument tissue that develops into the testa (Figs 1c, 2b).

In contrast to the gymnosperms, the angiosperm ovules and seeds are covered; they are enclosed inside the ovary. The ovary is the base of a modified leaf (carpel) or the fusion between several carpels in a pistil. A mature ovary contains one or more mature seeds and is called a fruit; a pericarp (fruit coat) develops from the ovary wall and can contain additional flower parts. Both seeds and fruits can be the dispersal units of angiosperms.

A hallmark of angiosperm reproduction is double fertilization; that is, in addition to the egg cell fertilization, a second fertilization event occurs in which the central cell nucleus of the megagametophyte is targeted by a second sperm cell nucleus (Floyd & Friedman, 2000; Baroux *et al.*, 2002; Friedman & Williams, 2004; Berger *et al.*, 2008; Friedman *et al.*, 2008; Friedman & Ryderson, 2009). This leads to the formation of the endosperm (Fig. 2). Since the central cell of most angiosperm species has either one (Nuphar/Schisandra-type) or two nuclei (Polygonum-type), the resulting fertilized endosperm is either diploid or triploid. The endosperm grows much more rapidly than the embryo, initially through cell size enlargement coupled with endopolyploidy (nuclear divisions without cytokinesis), followed by cellularization of each nucleus. The rate of seed growth decreases in angiosperms at this stage (Sundaresan, 2005).

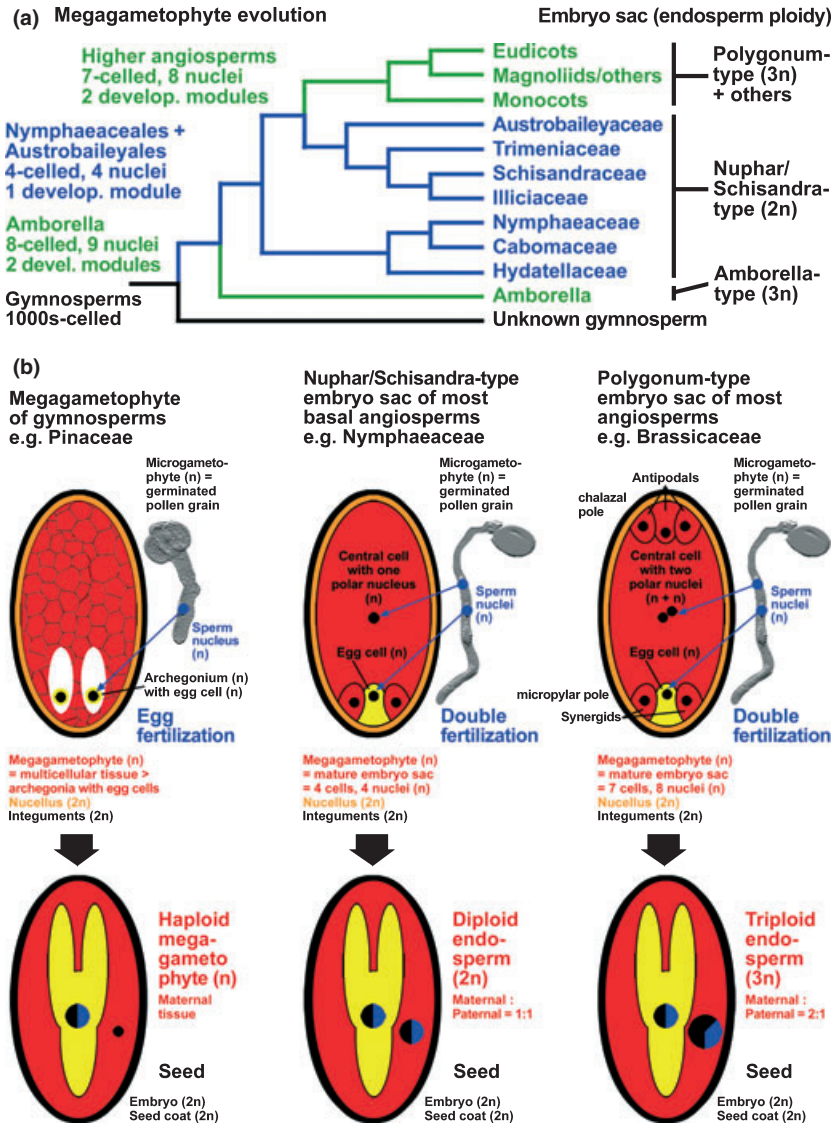

Fig. 2 Gymnosperm and angiosperm megagametophyte fertilization and the evolutionary history of the angiosperm embryo sac and endosperm. (a) Best hypothesis (Friedman & Ryderson, 2009) for the early evolution of the angiosperm megagametophyte. (b) Megagametophyte structure, fertilization and seed development of gymnosperms and angiosperms. The first angiosperms may have produced four-nucleate, four-celled megagametophytes (one developmental module). Double fertilization of the uninucleate haploid central cell in Nymphaeales and Austrobailyales yields diploid endosperms (Nuphar/Schisandra-type). In the common ancestor of all angiosperms except Amborella, Nymphaeales and Austrobailyales, insertion of a nuclear migration event at the two-nucleate syncytial stage led to initiation of two developmental modules and formation of a seven-celled, eight-nucleate female gametophyte (Polygonum-type). Modular duplication also occurred independently in the lineage to the Amborella-type embryo sac; in addition, asynchronous cell division in the micropylar module yields a third synergid in the *Amborella trichopoda* endosperm (Friedman & Ryderson, 2009). In addition to endosperm, perisperm in basal angiosperm seeds is known for Hydataceae, Nymphaeaceae, Cabomaceae and Trimeniaceae.

III. Evolution and functions of the endosperm tissue

Two major hypotheses for the origin of the endosperm have been proposed and are summarized by Friedman & Williams (2004). The hypothesis by Sargant (1900) suggests that in ancient seeds or seed-like structures the central cell used to be an additional gamete besides the egg cell. During fertilization, two embryos would have been produced in the ancestors of flowering plants, one of which evolved into the sterile endosperm tissue with nourishing function in the seeds of modern plants (Friedman, 1995). This hypothesis is supported by the fact that, in *Ephedra* and *Gnetum* (Gnetales, gymnosperms), several embryos develop in the growing seed (Friedman, 1992). Many phylogenetically basal angiosperms develop diploid endosperm (Fig. 2; Nuphar/Schisandra-type embryo sac), which further supports Sargant's (1900) theory. On the other hand, *Amborella trichopoda*, the most basal angiosperm, has triploid endosperm (Fig. 2a; Amborella-type embryo sac; Friedman & Ryderson, 2009). The currently prevailing phylogeny separates the Gnetales from the angiosperms, that is, it does not support the classical 'anthophyte hypothesis' that angiosperms and Gnetales share a direct common ancestor (see Section I 'Introduction'). Based on these observations, no unambiguous statement can be made.

The second hypothesis (Strasburger, 1900; Coulter, 1911) for the origin of the endosperm suggests that it represents a homolog of a portion of the gametophyte that later became sexualized. The second fertilization event of the central cell nucleus by an additional sperm nucleus cell might have provided some unknown fitness advantages to the growing embryo (Friedman & Williams, 2004). The endosperm would then have originated from mutations of

the female gametophyte, which predestine these cells for a supporting nonreproductive role. This would explain the occurrence of certain types of apomixes (Carman, 1997). According to Baroux *et al.* (2002), this theory is supported by the fact that the addition of the paternal genome to the maternal central cell might create hybrid vigor. Both of these hypotheses have justifications, but a definite origin of the endosperm tissue is still not clear (Berger, 2003; Friedman & Ryderson, 2009).

After fertilization in what is the most common type of endosperm development, the nuclear type, the initial endosperm nucleus divides repeatedly without cell wall formation, resulting in a characteristic coenocyte-stage endosperm (Baroux *et al.*, 2002; Olsen, 2004; Friedman & Ryderson, 2009). In many species, including *Arabidopsis thaliana* and cereals, this is subsequently followed by endosperm cellularization. Different developmental fate of chalazal and micropylar domains is a common pattern among the endosperms of all basal angiosperm taxa and suggests that this may be a feature of endosperm development in all angiosperms (Figs 13–16 in Floyd & Friedman, 2000). Interactions and endosperm–embryo signaling is suggested from the fact that the bipolar endosperm development pattern of most angiosperms is shared with the bipolar pattern of the embryos. For example, in all Nymphaeales (Fig. 2a; Nymphaeaceae, Cabomaceae, Hydatellaceae), the micropylar endosperm undergoes division and becomes cellularized, whereas the chalazal domain remains undivided and acts as a haustorium, sometimes extending into the perisperm (Floyd & Friedman, 2000; Rudall *et al.*, 2008, 2009). Other examples of bipolar endosperm development are the Brassicaceae *A. thaliana* and *Lepidium virginicum*, in which a multinucleated 'chalazal' region forms, and, at the same time, when the rest of the endosperm including the micropylar domain cellularizes, this chalazal region remains multinucleated (Nguyen *et al.*, 2000; Olsen, 2004). The radicle is embedded within the micropylar endosperm domain, whereas the tip of the cotyledons resides within the chazal endosperm domain of these Brassicaceae. The evolution of endosperm developmental patterns among basal flowering plants is reviewed in detail by Floyd & Friedman (2000), and endosperm development of other angiosperms is summarized by Baroux *et al.* (2002). The genera *Arabidopsis* and *Lepidium* emerged as highly suited for cross-species work on seeds and fruits within the Brassicaceae family (Müller *et al.*, 2006; Linkies *et al.*, 2009; Mummenhoff *et al.*, 2009).

Regardless of its origin, contemporary endosperm tissue serves not only as a nutrient source for the embryo during seed development, but also as an integrator of seed growth and development which includes reciprocal signaling between seed compartments and parental effects caused by imprinting (Berger *et al.*, 2006; Berger & Chaudhury, 2009; Otho *et al.*, 2009; Springer, 2009). The endosperm is, depending on the species, partially or fully obliterated upon seed maturity. However, most angiosperm species have retained an endosperm layer in their mature seeds (Fig. 19 in Floyd & Friedman, 2000; Fig. 3 in Forbis *et al.*, 2002; Fig. 4 in Finch-Savage & Leubner-Metzger, 2006). In many cases, this endosperm in the mature seed is also involved in the control of germination by being a barrier for the growing radicle. During germination, the micropylar endosperm weakens, allowing the radicle to protrude the surrounding tissues. The hypothesis that weakening of the seed covering layers is achieved by enzymatic action was first proposed by Ikuma & Thimann (1963). Endosperm weakening was originally demonstrated for seeds of asterid species with either a thick endosperm layer (tomato, tobacco, coffee) or a thin endosperm layer (e.g. lettuce; Ni & Bradford, 1993; Bewley, 1997a,b; Toorop *et al.*, 2000; Leubner-Metzger, 2002; Petruzzelli *et al.*, 2003; Nonogaki, 2006). More recent work demonstrated that endosperm weakening also occurs in seeds of rosid species. The Brassicaceae *Lepidium sativum* and *A. thaliana* have a thin endosperm layer and weakening of the micropylar endosperm was biomechanically quantified during the germination of *L. sativum* (Müller *et al.*, 2006; Bethke *et al.*, 2007; Linkies *et al.*, 2009). Comparison of the transcriptome of the micropylar and nonmicropylar endosperm of *L. sativum* supports the bipolar character of this seed tissue (Linkies *et al.*, 2009). It is the micropylar endosperm that can function as a barrier to radicle expansion and thereby can contribute to the regulation of germination timing. Finch-Savage & Leubner-Metzger (2006) proposed that at least some of the molecular mechanisms of endosperm weakening are widespread and are evolutionarily conserved traits.

IV. Evolution of dormancy

Seed dormancy is defined as an intrinsic block to the completion of germination of a viable seed under favorable conditions for germination (e.g. temperature, humidity, light) of the corresponding nondormant seed. Seed dormancy controls germination timing in response to the seasons and plays an important role in seed plant evolution and adaptation to climatic changes (Forbis *et al.*, 2002; Baskin & Baskin, 2004; Evans & Dennehy, 2005; Leubner-Metzger, 2007). Germination timing may strongly influence the rate at which species can expand their range, and may play an important role in determining survival or extinction during climate change (Donohue, 2005).

Baskin & Baskin (1998, 2004) have proposed a comprehensive ecophysiological classification system which includes five classes for 'whole seed' dormancy: physiological (PD), morphological (MD), morphophysiological (MPD), physical (PY) and combinational (PY+PD). These different classes and their distribution among angiosperms are also summarized by Finch-Savage & Leubner-Metzger (2006).

Morphological dormancy is evident in seeds with embryos that are differentiated but very small compared with the size of the entire seed. The embryo to seed ratio (E : S ratio) describes the relative size of the embryo within the seed. A high E : S ratio (e.g. 0.9) means that the embryo fills up most of the seed volume, whereas a low E : S ratio (e.g. 0.1) means that the embryo is tiny and the nutrient storage tissue (endosperm, perisperm, megagametophyte) fills up most of the seed volume (Figs 3, 4 in Forbis *et al.*, 2002; Figs 3, 4 in Finch-Savage & Leubner-Metzger, 2006). Seeds with low E : S ratios often have long (a month or more) germination times and the occurrence of abundant megagametophyte (e.g. cycads, gymnosperms, Fig. 1c) or perisperm plus endosperm (e.g. *Nuphar*, basal angiosperms, Fig. 1d) tissue are typical for MD-class seeds. Forbis *et al.* (2002) used ancestral state reconstruction methods of continuous characters using E : S family means for 179 families calculated from a large dataset of 1222 extant angiosperm species. Their analysis showed that the E : S ratios have increased in derived angiosperms compared with ancestral angiosperms. They proposed, based on these results, that a tiny embryo embedded in abundant endosperm/perisperm, and thereby classified as MD (and MPD), is the ancestral dormancy type of angiosperms. This hypothesis is in agreement with the results of Baskin & Baskin (2004). MD simply delays germination timing by the time the embryo needs to grow inside the seed before germination can take place. The dispersal of seeds with a small embryo that needs time to grow might have evolved as an ancient strategy to distribute germination times, since successful germination is highly dependent on environmental conditions.

Among basal angiosperms (Fig. 2a), seeds with abundant perisperm that occupies a larger portion than the endosperm storage tissue is characteristic for extant and extinct Nymphaeales (Nympheaceae, Cabomaceae, Hydatellaceae) (Floyd & Friedman, 2000; Friis *et al.*, 2001; Yamada *et al.*, 2001; Chen *et al.*, 2004; Baskin & Baskin, 2007; Friedman 2008; Rudall *et al.*, 2009) and Austrobaileyales (Trimeniaceae) (Yamada & Marubashi, 2003; Yamada *et al.*, 2008). The presence of perisperm as the only nutritive tissue in the seed is rare. It is usually present together with endosperm in various proportions, locations and shapes. Abundant perisperm is not restricted to basal angiosperms and is also not necessarily associated with MD. Abundant perisperm is typical for most Caryophyllales seeds, such as sugarbeet (nondormant, Amaranthaceae; Hermann *et al.*, 2007) and cacti (PD, Cactaceae; Stuppy, 2002).

A trend to higher E : S ratios is also evident for gymnosperms (Forbis *et al.*, 2002). For example, extant basal gymnosperms, particularly cycads (*Zamia*, *Cycas*, Fig. 1c) and ginkgos, have smaller embryos than some of the more derived gymnosperm taxa, such as *Callitropsis*, *Picea*, *Pinus* and *Juniperus* (Baskin & Baskin, 1998; Fig. 4 in Forbis *et al.*, 2002). Forbis *et al.* (2002) stated that available gymnosperm embryo fossils are approximately in the same shape and size ranges as extant gymnosperm embryos of related groups (see references cited in Forbis *et al.*, 2002) and that there are no fossil gymnosperm seeds with extremely small or extremely large E : S ratios. They therefore suggested that an unknown gymnosperm ancestor that predates these fossil specimens likely had a small embryo at dispersal. As several extant taxa have much larger embryos, they interpreted this as support for the hypothesis of increasing E : S ratios among gymnosperms.

Taken together, there seems to be a general trend of increasing relative embryo size during evolution (higher E : S ratio) for both angiosperms and gymnosperms (Forbis *et al.*, 2002; Baskin & Baskin, 2004). Based on this, Forbis *et al.* (2002) proposed that morphological dormancy is the ancestral dormancy type among gymnosperms and angiosperms. This is consistent with the conclusion reached by Baskin & Baskin (1998, 2004). The evolution of larger embryo size likely resulted in occurrence of nondormant seeds; the embryo did not need to grow before germination. It is thought that increased relative embryo size is one of the main determinants (or requirements) for the evolution of other classes of seed dormancy (Finch-Savage & Leubner-Metzger, 2006).

The core eudicots tend to have less endosperm than more basal extant angiosperm species. At the same time, physiological dormancy developed, which is thought to be linked to adaptation to seasonal weather changes as its release requires that the seeds perceived a specific environmental trigger(s). PD is the most abundant type of dormancy and is found in seeds of all major gymnosperm and angiosperm clades (Fig. 1 in Baskin & Baskin, 2004; Fig. 4 in Finch-Savage & Leubner-Metzger, 2006). PD can be divided into different types; the most common form in both angiosperm and gymnosperm is nondeep PD. Embryos excised from seeds with nondeep PD will germinate normally and treatment with gibberellins (GA) will break dormancy. Also, depending on species, dormancy can be broken by scarification (abrasion or cutting of the covering layers), after-ripening (a period of air-dry storage), and cold or warm stratification. It has been shown that nondeep PD is determined by physiological factors in both the embryo and/or the covering layers ('coats' in a loose sense) (Bewley, 1997a,b; Koornneef *et al.*, 2002; Kucera *et al.*, 2005; Nonogaki, 2006; Bentsink & Koornneef, 2008; Holdsworth *et al.*, 2008). Coat dormancy is mediated by any of the covering layers (the endosperm and/or the testa). Embryos excised from coat-dormant seeds develop and grow readily. Abscisic acid (ABA) is an important positive regulator of the coat-mediated nondeep PD in the seeds of both gymnosperms and angiosperms (Kucera *et al.*, 2005). This suggests that gymnosperms and angiosperms share common ABA-related molecular mechanisms regulating dormancy and germination, and that ABA dependency is a

plesiomorphic trait for angiosperms and gymnosperms. The ABA-related transcription factor *ABI3/VP1* (*ABA INSENSITIVE3/VIVIPAROUS1*) is widespread among green plants and is involved in regulating dormancy of angiosperm and gymnosperm seeds and buds (Holdsworth *et al.*, 2008; Graeber *et al.*, 2009). By contrast, *DOG1* (*DELAY OF GERMINATION 1*), a major quantitative trait gene more specifically involved in seed dormancy and germination timing, is so far only known within the Brassicaceae and its relation to ABA is the subject of ongoing research (Bentsink *et al.*, 2006; Graeber *et al.*, 2009).

Physiologically dormant and nondormant seeds are distributed over the entire phylogenetic tree of gymnosperms, basal angiosperms, and eudicots (Fig. 4 in Finch-Savage & Leubner-Metzger, 2006). Therefore it has been proposed that the gain and loss of PD quite likely occurred at several times during evolution (Baskin & Baskin, 1998; Finch-Savage & Leubner-Metzger, 2006). The evolution of PD also led to the appearance of MPD in seeds with a small embryo, which upon gain in embryo size and concurrent loss of MD led to PD seeds (Fig. 5 in Finch-Savage & Leubner-Metzger, 2006). The most phylogenetically restricted dormancy classes are PY and a combination of both PY and PD (Baskin & Baskin, 1998, 2004; Finch-Savage & Leubner-Metzger, 2006). PY is characterized by a water impermeability of the seed or fruit coat. It is believed to be an adaptation of the plant to specialized life habitats (Baskin & Baskin, 2004). PY is not found in gymnosperms, but only in angiosperm seeds, which indicates that it is a more derived form of dormancy.

V. Early seed-like structures and the transition to seeds

The origin and evolution of the seed habit is a fascinating story that started in late Devonian *c.* 370 million yr ago (Ma). Three major evolutionary trends were important for the transition from the progymnosperms to the seed plants (Niklas, 1997; Doyle, 2006; Taylor & Taylor, 2009): the evolution from homospory to heterospory, meaning the production of specialized haploid female-like megaspores and male-like microspores; the evolution of the integuments; and the evolution of pollen-receiving structures. This includes the transition to water-independence of the pollination process.

The earliest seed plants emerged in the late Devonian from a paraphyletic group termed progymnosperms (Fig. 1a). Progymnosperm fossils show vegetative structures typical for seed plants combined with pteridophytic reproduction. Seed-like structures relating to the progymnosperm/seed–plant transition are often not preserved in fossil specimens and/or cannot be assigned unambiguously to the fossil specimen. *Archaeopteris*, an extinct progymnosperm, was the first known modern tree (Judd *et al.*, 2002; Crane *et al.*, 2004). Although it produced spores rather than seeds (Niklas, 1997; Judd *et al.*, 2002), it exhibited an advanced system of spore production called heterospory. Heterospory, which has probably evolved independently in several lineages, is widely believed to be a precursor to seed reproduction.

Fossils of paraphyletic seed ferns (Lyginopteridopsida, Fig. 1a) exhibit a variety of seed-like structures (Hemsley, 1993; Taylor & Taylor, 1993, 2009; Doyle, 2006). The oldest fossil pre-ovules are from the Middle Devonian (385 Ma, e.g. *Runcaria*; Gerrienne *et al.*, 2004). *Elksinia polymorpha*, the oldest known fossil seed plant, is a seed fern from the Late Devonian (Taylor & Taylor, 1993; Niklas, 1997; DiMichele *et al.*, 2006). This suggests that seed plants arose between 385 and 365 Ma, in the time interval separating *Runcaria* and the earliest known seed plants. The seed ferns *Elksinia*, as well as *Archaeosperma* and *Lagenostoma*, produced pre-ovules or ovules on sterile structures called cupules (Fig. 1a, inset). Cupules are cup-like structures that partially enclose the ovule. In these early ovules, the nucellus was surrounded by integumentary tissue consisting of free lobes (Fig. 1a, inset). These lobes curved inwards at their tips, forming a ring around the apical end. So far, embryos have not been found in Devonian seed fern fossils.

The medullosan seed ferns are thought to be a monophyletic group of seed plants (Judd *et al.*, 2002; Crane *et al.*, 2004; DiMichele *et al.*, 2006) and were abundant trees in Carboniferous floodplains (> 290 Ma) and extended well into the Permian (> 250 Ma; Fig. 1a). This group includes *Stephanospermum* (Fig. 1b), *Trigonocarpus, Pachytesta*, *Rhynchosperma*, *Medullosa*, and *Polypterospermum* (Combourieu & Galtier, 1985; Drinnan *et al.*, 1990; Taylor & Taylor, 1993; Dunn *et al.*, 2002). Fossil seeds from medullosan seed ferns are several mm to cm long. In some cases, even embryo structures have been preserved. In these seed ferns, the cupule was replaced by a three-layered testa (Fig. 1b). There are indications that multiple origins of cupules existed and that structures called cupules are not all homologous among Paleozoic and Mesozoic seed ferns or gymnosperms (Hemsley, 1993; Doyle, 2006; Taylor & Taylor, 2009). The ovules usually have a round shape, with one end of the integument drawn out into a micropyle that probably helped guide pollen to the megagametophyte (Fig. 1b).

Schmeissneria has been proposed by Wang *et al.* (2007) as an Early Jurassic (> 160 Ma) missing link to angiosperms because it has angiospermous traits like closed carpels. This proposal is not widely accepted, however, and *Schmeissneria* is proposed by others to be a member of the Ginkgoales (Kirchner & Van Konijnenburg-Van Cittert, 1994; Zhou, 2009). Phase-contrast X-ray microtomography links charcoalified fossil seeds from the Early Cretaceous (144 to 100 Ma) with the gymnosperm Gnetales and Bennettitales

(Friis *et al.*, 2007, 2009). These fossil seeds are *c.* 0.5–1.8 mm long and have two distinctly different layers surrounding the nucellus: an inner, thin, membranous integument, formed by thin-walled cells; and a robust, outer, sclerenchymatous seed envelope that completely encloses the integument except for the micropylar opening. This outer seed envelope with distinctive anatomical structure surrounds the nucellus and the integument. The integument is extended apically into a long, narrow micropylar tube. Only Gnetales (extant and extinct), Erdmanithecales (extinct) and Bennettitales (extinct) are known to have seeds with an additional seed envelope and the integument extended into a long, narrow micropylar tube. The interpretation of the outer covering layer of Bennettitales seeds as an extra-integumentary outer envelope, as it is known from Gnetales seeds, is a matter of considerable debate (Friis *et al.*, 2007, 2009; Rothwell *et al.*, 2009).

Archaefructus, originally thought to be a stem-group angiosperm of Jurassic age, is not; the fossil specimens have been redated as belonging to the Early Cretaceous (*c.* 125 Ma) flora of China (Sun *et al.*, 2002; Friis *et al.*, 2003; Frohlich & Chase, 2007). It seems to have been an aquatic plant and had fruits (*c.* 10 mm long and 2 mm wide) that contained two to 12 small seeds. It is possible that *Archaefructus* is on the stem lineage to angiosperms, but evidence for this is ambiguous (Friis *et al.*, 2003; Pennisi, 2009). *Amborella trichopoda*, an obscure shrub found only in New Caledonia, emerged as a crucial window to the past (Friedman & Ryderson, 2009; Pennisi, 2009; Williams, 2009). *Amborella* sits at the base of the angiosperm family tree, the sister group of all other extant angiosperms (Fig. 2a). The nuclear genome sequence of *A. trichopoda* will be an exceptional resource for comparative plant genomics (Soltis *et al.*, 2008) and, based on its triploid endosperm (Fig. 2a), for re-examination of the evolutionary developmental history of the embryo sac (Williams, 2009).

VI. Seed size evolution

Seed size (mass) is central to many aspects of plant ecology and evolution (Harper *et al.*, 1970; Westoby *et al.*, 1996; Leishman *et al.*, 2000; Moles *et al.*, 2005a,b). During a period of rapid angiosperm diversification (85–65 Ma), angiosperms moved out of the tropics and shifted from being predominantly small-seeded to having a much wider range of seed sizes (Eriksson *et al.*, 2000; Moles *et al.*, 2005a,b). Extant angiosperms have seed masses spanning >11 orders of magnitude, from the lint-like seeds of orchids up to the 20 kg seeds of the double coconut (Harper *et al.*, 1970; Moles *et al.*, 2005a,b). Gymnosperms have somewhat less variation in mass, but have larger seeds than the average angiosperm (Fig. 3). Interestingly, individual orders and families vary by up to eight orders of magnitude (Fig. 3). Moles *et al.* (2005a,b) found that plant size is the strongest correlate with seed mass across a diverse assemblage of plant species (stronger than mode of dispersal or environmental conditions). Several authors have suggested that species with large seeds have an advantage under low light conditions, when their greater protein and lipid reserves, or their more advanced development, can facilitate growth (Salisbury, 1942; Mazer, 1989; Rees & Westoby, 1997; Geritz *et al.*, 1999; Eriksson *et al.*, 2000; Leishman *et al.*, 2000; Moles *et al.*, 2005a,b; Bruun & Ten Brink, 2008). However, large seeds usually come at the cost of seed number per flower or fruit (Leishman, 2001). In addition, large seeds cannot be physically borne on small plants because of the weight of the seed, which may partly explain the association between plant size and seed size (Grubb *et al.*, 2005).

Another hypothesis to explain the plant size/seed size correlation is that there are common genetic components that determine seed size, plant size, and the size of other plant organs. There have been several recent reviews concerning the genetic determinants of organ size (Sundaresan, 2005; Anastasiou & Lenhard, 2007; Bogre *et al.*, 2008; Busov *et al.*, 2008; Krizek, 2009). More cells or larger cells could both lead to larger organs, but in general it appears to be a combination of both (we will review several examples in the following paragraphs). Cell cycle times, and the length/duration of developmental periods, are therefore important factors determining final organ size. In angiosperm seeds, the size of each of the three major compartments (embryo, endosperm/perisperm, and seed coat) could increase individually. However, the growth of these organs is generally coordinated (Sundaresan, 2005; Otho *et al.*, 2009), so selection for increased embryo size, may lead to a larger endosperm as well, and perhaps have consequences in other organs.

As with most developmental processes, the action of transcription factors has been shown to play a key role in determining seed size. For example, in *A. thaliana*, large seeds can be generated by mutations in the *APETALA2 (AP2)* transcription factor (Jofuku *et al.*, 2005; Ohto *et al.*, 2005). Similarly, ectopic expression of the *AINTEGUMENTA (ANT)* transcription factor can also lead to larger seeds (Krizek, 1999; Mizukami & Fischer, 2000). Luo *et al.* (2005) found that mutations in either *HAIKU2* (*IKU2*) or *MINISEED3* (*MINI3*) led to reduced seed size, and that the mutant seed phenotypes depended on the parent-of-origin genotype of the endosperm and embryo. *MINI3* is a *WRKY* family transcription factor, and *IKU* is a leucine-rich repeat (LRR) receptor kinase. *IKU2* is expressed only in the endosperm, while *MINI3* is expressed in both the endosperm and the embryo. *IKU2* expression was down-regulated in *mini3* mutants, indicating that *MINI3* acts upstream of *IKU2*. The reduced seed size of *iku* mutants showed reduced endosperm growth, premature cellularization of the endosperm, and a reduced proliferation of the embryo after the early torpedo stage (Garcia *et al.*, 2003).

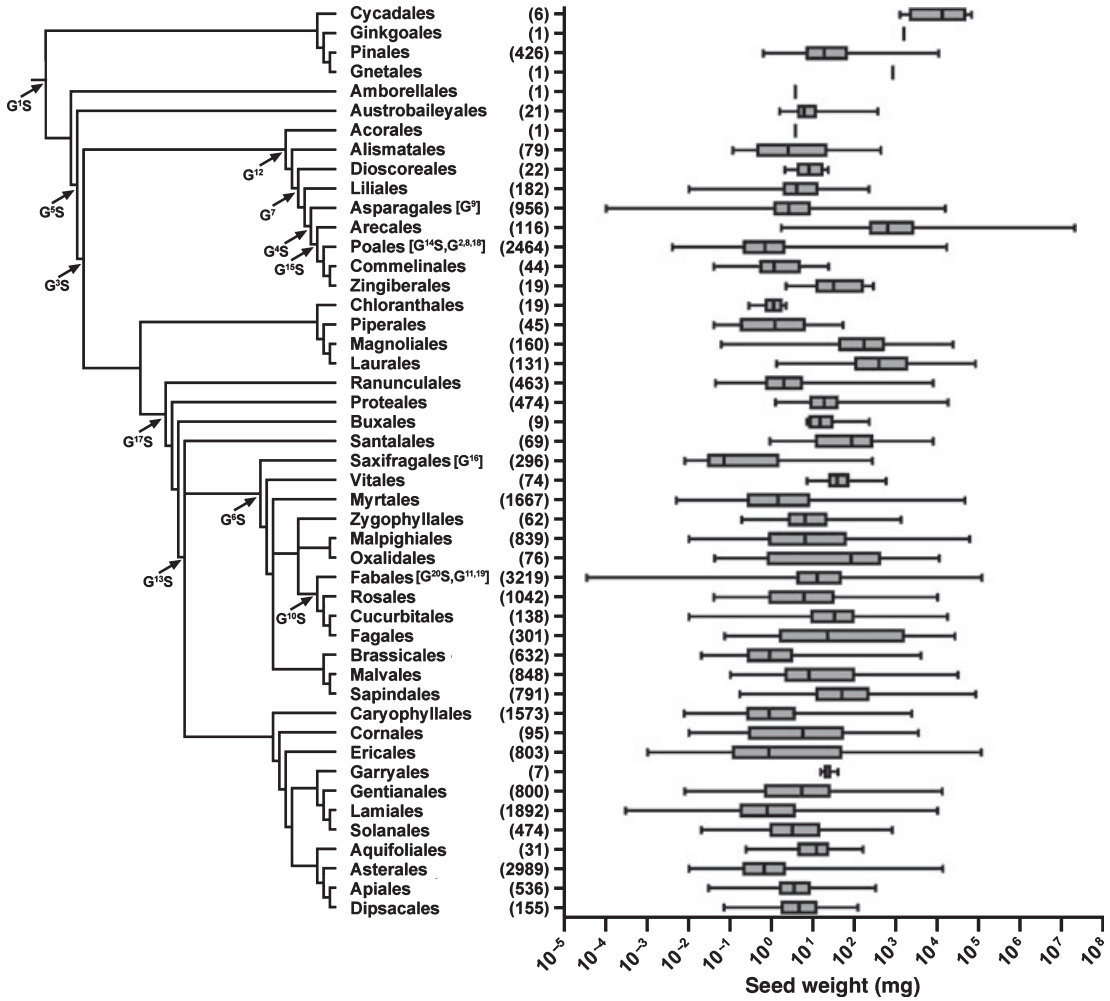

Fig. 3 Comparison of variation in seed mass of different plant species. Shown is a phylogeny of seed plants to the order level, and the corresponding seed masses are figured as whisker-box-plots. The gray boxes include 50% of all data points for a certain order, with the vertical line showing the median and the error bars indicating the range of seed masses. Numbers in round brackets indicate the number of species in the corresponding order for which seed mass data were available. Arrows in the phylogenetic tree indicate major divergence points in genome size (G) and seed mass (S). Shown are the 20 largest contributions to present-day variation in 2C DNA content, ranked from 1 to 20 (superscript numbers following G) by their contribution score for genome size (Beaulieu *et al.*, 2007). Major significant divergences for seed mass are shown (Moles *et al.*, 2005a; Beaulieu *et al.*, 2007). Note that often genome size and seed mass divergence points belong to the same node. Genome size and seed mass divergences that are within an order are shown in brackets directly behind the order's name. All seed mass data are from Liu *et al.* (2008). The phylogenetic tree was constructed using Phylomatic (http://www.phylodiversity.net/phylomatic).

Zhou *et al.* (2009) recently discovered that *SHORT HYPOCOTYL UNDER BLUE* (*SHB1*) regulates seed development through changes in cell size and number. Kang & Ni (2006) found a mutant, *shb1-D*, that was a dominant gain-of-function allele that led to overexpression of *SHB1*. When Zhou *et al.* (2009) studied phenotypic effects in the seed, they found that *shb1-D* exhibited increased seed mass largely as a result of coordinated endosperm cellularization and enlargement and continued embryo development. The *shb1-D* mutants had more cells, larger cells, accumulated more proteins and fatty acids, and had delayed embryo development (which was compensated for later in embryogenesis). By utilizing chromatin immunoprecipitation (ChIP), Zhou *et al.* (2009) were able to show that *SHB1* associates with *MINI3* and *IKU2* promoters, which indicates that these genes may all act in a coordinated fashion to affect final seed mass through the proliferation or delay of endosperm and embryo development.

Xiao *et al.* (2006) discovered changes in *Arabidopsis* seed mass that were associated with mutations in *METHYLTRANSFERASE 1* (*MET1*) and *DECREASE IN DNA METHYLATION1* (*DDM1*). Pistils of *met1-6* or *ddm1-2* mutants pollinated with wild-type pollen produced F_1 plants with hypomethylated maternal genomes. Seeds from these F_1 plants showed delayed endosperm development, and larger endosperm volume compared with the wild-type

plants. A reciprocal cross (paternal *ddm1-2* or *met1-6* with a wild-type mother) produced F_1 seeds with a hypomethylated paternal genome, which resulted in early embryo cellularization, and consequently a smaller endosperm volume. These experiments show that parent-of-origin genotype, and methylation affect the final size of seeds, and that changes in endosperm volume can affect final seed size, even though the endosperm is largely consumed by the embryo during *Arabidopsis* seed maturation.

Unlike the previous studies, which largely identified *Arabidopsis* mutants, resulting in either delayed or continued endosperm or embryo development, Schruff *et al.* (2006) found a mutation that resulted in dramatically enlarged seeds caused by extra cell divisions in the integuments, which resulted in an enlarged seed coat. The mutation was a loss-of-function in *AUXIN RESPONSE FACTOR 2* (*ARF2*), which is a member of a family of transcription factors that bind to auxin-responsive elements. The wild-type *ARF2* generally functions to repress cell division, but a mutant of *ARF2*, *megaintegumenta (mnt)*, continues cell division in the integument, leading to an enlarged embryo sac. Similarly, Adamski *et al.* (2009) found that *KLUH* (*KLU*) regulates seed size in the same manner; it stimulates cell proliferation in the integument, thus determining the growth potential of the seed coat and seed. In both cases (*ARF2* and *KLU*), the effects were dependent on the parent-of-origin genotypes of the endosperm and embryos. Similarly, a mutant of *APETALA2* (*AP2*) produced larger seeds, with larger integument cells (Otho *et al.*, 2009). This was accompanied by an extended period of rapid endosperm growth. Conversely, instead of integument cell elongation, Garcia *et al.* (2003, 2005) found an *Arabidopsis* mutant of *TRANSPARENT TESTA GLABROUS* (*TTG2*), which resulted in a reduction of integument cell elongation, and smaller seeds. Perhaps the size of the embryo sac partly determines the final size of the seed. Supporting this conclusion is the work of Fukuta *et al.* (2005), who showed that physical restriction in small pods led to seed size reduction in a brassinosteriod-deficient *Vicia faba*.

Outcomes of these studies seem to agree with a general theory of organ growth that consists of two phases (Anastasiou & Lenhard, 2007; Bogre *et al.*, 2008). In the first phase, cell proliferation is coupled with cell growth, leading to an increase in cell number within the developing organ. In the second phase, cell division ceases and further growth of the organ results from cell expansion. We have reviewed several mutations (*met1-6*, *ddm1-2*, *iku2*, *mini3*, and *arf2*) that have led to continued cell proliferation. And we have also reviewed mutations that cause changes in cell expansion or final cell size (*ap2* and *ttg2*). But final organ size is determined at an integrated organismal level. For example, if cell division is disrupted as a result of mutation, the reduction in cell numbers may be accompanied by increased cell size, a phenomenon termed 'compensation' (Garcia *et al.*, 2005; Horiguchi *et al.*, 2006). Also, putative mobile growth regulators, such as generated by *Arabidopsis KLUH* (*KLU*), act at the periphery of organs (such as leaves and flowers) and can either increase or decrease cell proliferation in the organ meristem. Anastasiou *et al.* (2007) suggested that such expression at the margin could provide a readout for the perimeter to area ratio of an organ. Other classes of growth regulators, such as the *Arabidopsis TOR* gene (*atTOR*; Menand *et al.*, 2002) and the ubiquitin-mediated growth factor *BIG BROTHER* (*BB*; Disch *et al.*, 2006), operate in a similar manner to control cell proliferation in a dosage-dependent manner.

Interestingly, the major changes in seed size have been associated with changes in genome size (Beaulieu *et al.*, 2007). Genome size varies over four orders of magnitude in plants (Bennett & Leitch, 2005). The amplification of transposable elements and polyploidy are both thought to be common mechanisms for increasing nuclear DNA amount across species (Bennetzen, 2002; Kidwell, 2002; Bennetzen *et al.*, 2005; Soltis *et al.*, 2009). Polyploidy has been a particularly pervasive factor in angiosperm evolution (Soltis *et al.*, 2009). Beaulieu *et al.* (2007) found that divergences in seed mass have been more closely correlated with divergences in genome size than with divergences in other morphological and ecological variables (Fig. 3). Plant growth form is the only variable examined thus far that explains a greater proportion of variation in seed mass than does genome size. Yet the functional consequences of genome size evolution remains a significant, unanswered question (Knight *et al.*, 2005; Knight & Beaulieu, 2008).

Why do species with larger genomes have larger seeds? There is a general trend for species with larger genome sizes to have larger cells and slower cell division rates (Francis *et al.*, 2008; Knight & Beaulieu, 2008; Gruner *et al.*, in press). Beaulieu *et al.* (2008) demonstrated a broad scale correlation between genome size and guard cell size across a wide range of angiosperms. In seeds, comparable cells in diploid and tetraploid species should have dramatically different cell sizes (interestingly, detailed comparisons of seed anatomy in ploidy series have not been made, to our knowledge). We propose that genome size increases may lead to a disruption of signal transduction networks. We have reviewed several transcription factors that have significant effect on seed size when mutated (*AP2*, *ANT*, *MINI3*, *ARF2*, *KLU*, *TOR* and *BB*). The end result of genome size change for seed development may be similar to when these transcription factors have undergone loss-of-function mutations, which can lead to changes in cell proliferation or timing of developmental periods (reviewed earlier in the paper). In our view, increased genome size may disrupt transcription factor binding, perhaps making it slower (from the sheer volume of DNA that must be 'read', or

because of a greater frequency of mismatches). Changes in genome size may be analogous to changes in methylation observed in the DDM1, MET1 mutants. Changes in nuclear DNA content brought about by polyploidy lead to variation in gene dosage and a doubling of orthologous genes in the genome. Interestingly, orthologous genes have been observed to be down-regulated by methylation in polyploids (Lee & Chen, 2001; Wang *et al.*, 2004, 2006).

The studies reviewed here were largely done using *Arabidopsis*. These studies should become the basis of a larger cross-species comparison to see if the genetic factors that have been identified in mutant studies of *Arabidopsis* are the same ones that have led to the profound variation in seed mass across the angiosperms. Whether these mechanisms are conserved in gymnosperms should also be tested.

VII. Conclusion

The evolution of the seed represents a remarkable transition for photosynthetic organisms. Here, we have reviewed the development and dormancy of seeds, the rise and fall of the endosperm, and the genetic mechanisms and developmental anatomy of large and small seeds. We would like to end by presenting a series of unanswered questions that are ripe for further research in the field of seed biology. Whether genome size increases lead to a disruption of signal transduction networks, causing continued cell proliferation and therefore seed enlargement, is first on our list. We would also like to know the biomechanical forces required to achieve embryo growth, endosperm weakening, testa (seed coat) rupture, and the genes that are either up-regulated or down-regulated during these transitions. How does variation in cell size (and genome size) affect germination, growth, and seed development? Why do some species have deep dormancy and others have nondeep dormancy, and what genes are responsible for these differences? Are the mechanisms that have led to the profound variation in seed mass across the angiosperms the same as the factors that have been identified in mutant studies of *Arabidopsis*? There is still much to be learned from the comparative anatomy and development of seeds. We suspect that when looking at seeds of two species that vary considerably in size, the species with larger seeds will have more fully developed embryos with a greater number of cells per embryo; larger cells in general; and will take longer to develop to compensate for a slower cell division rate. Indeed, Leishman *et al.* (2000) found a close relationship between whole-plant relative growth rates (RGRs) and seed mass, but whether whole-plant RGR is correlated with embryonic developmental rates in seeds is unknown. Many of the questions presented here are ideal for applying an integrative, phylogenic-based, cross-species, systems biology approach. And we predict great advances for our understanding of seed biology and evolution in the coming decade.

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