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# Tissue and cellular mechanics of seeds

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Distinct plant seed/fruit structures evolved to support reproduction and dispersal in distinct environments. Appropriate biomechanical properties and interactions of the various seed compartments are indispensable to plant survival. Most seeds are dispersed in a dry state generated during seed development/maturation for which novel aspects of endosperm–embryo interaction were discovered. The various layers covering the embryo of a mature seed define the patterns of water uptake during germination. Their biomechanical weakening together with embryo cell expansion is mediated by cell wall remodelling to facilitate radicle protrusion. Recent work with different species has revealed mechanisms underpinning specific embryo growth zones. Abiotic and biotic factors were shown to release different types of seed and fruit coat-mediated constraints to water uptake and germination.

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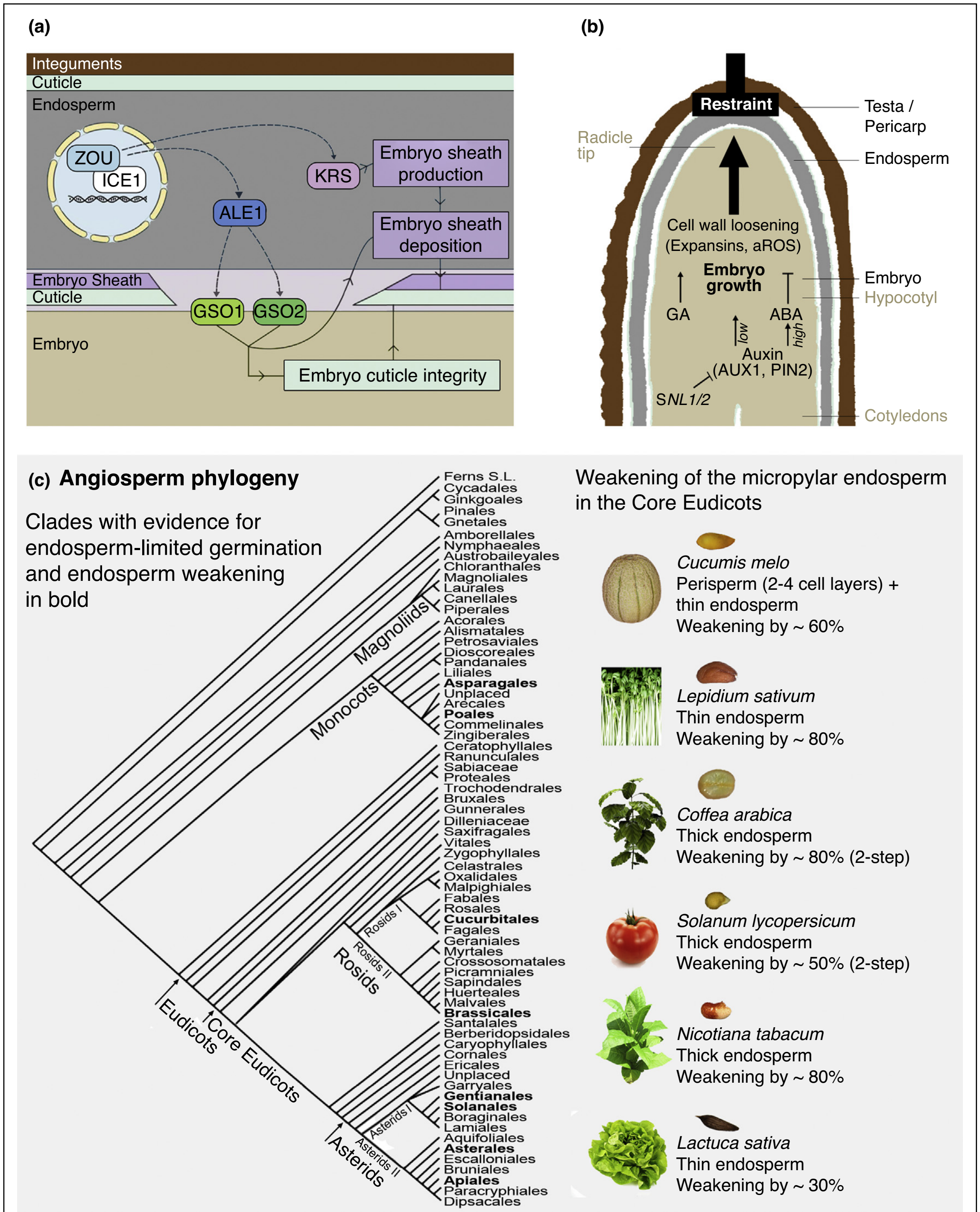
## Introduction

Seed germination is a complex process and we need to understand the underlying molecular, hormonal and mechanical aspects. At maturity, a typical angiosperm diaspore (seed/fruit) consists of an embryo and its 'coats', which might include living endosperm, dead testa (seed coat derived from the outer integument) and pericarp (fruit coat). Mechanical interplay between different seed compartments is a crucial factor from seed development to the completion of germination. New insights into the mechanical interactions between embryo and endosperm during seed development have revealed a key role of the transcription factor ZHOUPI [1••]. The endosperm, seed and fruit coats are a major mechanical constraint to embryo expansion. Germination is triggered by the uptake of water into the 'dry' seed and new techniques made it possible to track the water entering a seed with a holistic *in vivo* approach [2•]. Plant cell wall loosening and weakening of the various 'coats' mediate embryo growth and radicle protrusion. These processes are under the control of hormones including gibberellins (GA), abscisic acid (ABA), ethylene, jasmonates, nitric oxide and auxin [3••,4,5,5a]. Advanced imaging enables 3D monitoring of embryo growth *in planta* to reveal distinct spatiotemporal patterns on the cellular level and the influence of plant hormones [6••]. Fruit coats can confer dormancy by hindering water-uptake or by acting directly as a mechanical constraint [7••]. Seed biology is a major research topic of importance for food security and climate change [5,8,9]. Plant biomechanics can be defined as the study of the structure and function of plant systems (such as seeds) by the application of concepts and methods from mechanics; for terms and definitions see [9a]. Integrating molecular, epigenetic, morphological and biophysical aspects are key to advance our understanding of the complex process of seed germination.

## The mechanics of embryo and endosperm interaction during seed development

All events during seed development and seed germination are finely tuned and coordinated. A seed is formed from a fertilised ovule and consists in the mature stage of seed coat, embryo and a food storage compartment. Food storage can either be in the cotyledons (embryonic leaves, e.g. *Pisum sativum*) or the endosperm, the nutritive tissue of most angiosperms [5]. The triploid endosperm arises from the fusion of a paternal sperm nucleus with two maternal polar nuclei, while the second paternal sperm nucleus fuses with the egg cell nucleus forming the embryo (double fertilisation) [10,11]. Endosperm development differs among species but in principal it can be divided in formation, cellularisation, differentiation, maturation and cell death. Endosperm formation and expansion is the major stimulus driving the early seed growth, which is restricted by the outer seed coat. It has been shown that seed turgor, leading to seed expansion is generated by the endosperm [12]. Auxin is necessary for normal endosperm and seed coat development [13]. During *Arabidopsis thaliana* seed development the endosperm undergoes programmed cell death to make space for the growing embryo [1••,11]. This endosperm breakdown is mediated by the transcription factors ZHOUPI and ICE1 (Figure 1a) [1••,14]. ZHOUPI triggers cell death by regulating cell wall remodelling proteins (CWRP), altering the mechanical properties of the endosperm and thus allowing the embryo to compress the surrounding endospermic tissue. *ZHOUPI* is exclusively expressed in the endosperm and is also involved in the

**Figure 1**

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The mechanics of embryo and endosperm interaction during seed development and germination. **(a)** A model for ZOU-dependent sheath formation during early seed development, after [16•] ©ASPB. ZOU regulates expression of ALE1 and KRS. ALE1 and the GSO1/GSO2 kinases ensure normal embryo cuticle formation. KRS is necessary for the production of an embryo sheath that surrounds the embryo. The mechanical and molecular interplay between endosperm and embryo is essential for normal seed development. **(b)** Schematic of the interplay between the growing embryonic axis and the surrounding seed 'coats' (endosperm and where applicable testa and/or pericarp) in a mature seed during germination. Gibberellins (GAs) promote cell wall loosening, thereby facilitating endosperm weakening. Abscisic acid (ABA) inhibits this process. Auxin influences the germination in a dose-dependent matter. Low concentrations promote germination and AUX1 is a key factor downstream of SNL1 and SNL2 [3]. High concentrations inhibit germination via an ABA–auxin interaction [46]. Elongation of the embryonic axis requires auxin