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## REVIEW ARTICLE

# The sticky tale of seed coat mucilages: production, genetics, and role in seed germination and dispersal

Tamara L. Western\*

Biology Department and Developmental Biology Research Initiative, McGill University, 1205 avenue Docteur Penfield, Montreal, QC H3A 1B1, Canada

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### Abstract

The production of hydrophilic mucilages by the seed coat or pericarp, which are released upon seed hydration, is a commonly found adaptation in angiosperms, known as myxodiaspory. These are composed primarily of pectins and hemicelluloses that undergo substantive swelling upon hydration. Synthesized in the Golgi apparatus and secreted to an apoplastic space via secretory vesicles, mucilages can also contain cellulose microfibrils or cellulosic fibres that are synthesized at the plasma membrane in association with microtubules. Investigation of mucilage production in, and differentiation of, the mucilage secretory cells of the genetic model plant *Arabidopsis thaliana* has identified a number of regulatory genes and enzymes involved in pectin synthesis and secretion, *in muro* pectin modification and secondary cell wall synthesis. Studies of the role of mucilages in both a number of species and in *Arabidopsis* mutants affected in its production suggest that they have multiple ecological roles. These include facilitation of seed hydration, mediation of germination under waterlogged conditions, prevention of seed dispersal or predation by adherence to soil, and promotion of seed dispersal by attachment to animals. The precise role of mucilages appears to be dependent on species and their environmental context.

**Keywords:** *Arabidopsis*, germination, mucilage, pectin, seed coat, seed dispersal, testa

### Introduction

Double fertilization in angiosperms leads not only to the commencement of embryogenesis and development of the nutritive triploid endosperm, but also the differentiation of the surrounding ovule integuments to become the mature seed coat. Changes to the coat include specializations to enable protection of the embryo as well as to facilitate dispersal and eventual germination. These can include mechanical reinforcement through the synthesis of secondary cell walls that may be impregnated with impermeable polymers such as lignin or suberin, or synthesis of secondary metabolites often visible as pigments (e.g. polyphenolics) that may aid in protection from pathogens. Another common specialization is the deposition of a hydrophilic, pectinaceous mucilage in the seed coat epidermis or surrounding pericarp developed from ovary tissue (i.e. fruit) (Grubert, 1974; Fahn, 1982; Boesewinkel and Bouman, 1984). The production of seed mucilage, known as myxospermy, occurs in a broad range of plants, from the Acanthaceae to the Brassicaceae to the Linaceae to the Plantaginaceae, while myxocarpy (fruit mucilage) occurs in families such as the Asteraceae, Lamiaceae and Poaceae (Grubert, 1974; Fahn, 1979; Grubert, 1981; Ryding, 2001; Kreitschitz, 2009). Mucilage is deposited into the apoplast of epidermal cells during differentiation of the seed coat or pericarp, and is released in response to seed hydration to form a water-containing, gel-like capsule surrounding the seed. Myxodiaspory (mucilage production by the seed dispersal unit, i.e. seed coat or pericarp) has been proposed to play a number of roles, including facilitation of seed hydration, regulation of germination by affecting oxygen entry into the seed, and mediation of seed dispersal through adhesion to soil or animal vectors (Grubert, 1974; Fahn, 1982; Ryding, 2001; Kreitschitz, 2009).

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\*Correspondence  
Fax: 1-514-398-5069  
Email: tamara.western@mcgill.ca