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Seed-coat anatomy and proanthocyanidins contribute to the dormancy of *Rubus* seed

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ABSTRACT

Rubus seed has a deep double dormancy that restricts germination due to seed coat structure and chemical composition. Improved germination of diverse *Rubus* species required for breeding improved blackberry and raspberry cultivars is partly dependent on the seed coat structure. This study evaluated the seed coat structure of three species with thin (*R. hoffmeisterianus* Kunth & C. D. Bouché), medium (*R. occidentalis* L.) and thick (*R. caesius* L.) seed coats. The three species exhibited distinctive seed-coat cell composition. The very thin testa (0.086 mm) of *R. hoffmeisterianus* had little exotesta (surface) reticulation; with the meso- and endotesta composed of sclereids of homogenous shape and size. *R. occidentalis* had a thick testa (0.175 mm) and a highly reticulate exotesta; the meso- and endotesta were composed of several diverse types of sclereids. *R. caesius* had the thickest seed coat (0.185 mm) but only moderate exotesta reticulation; the meso- and endotesta were composed of large, irregular, loosely arranged sclereids. *R. occidentalis*, a medium size seed, was the most heavily lignified with seed-coat thickness similar to *R. caesius*, the largest seed. Proanthocyanidins (PAs) from dry seed of six *Rubus* species were extracted and quantified by high performance liquid chromatography. *R. hoffmeisterianus*, a thin only slightly hard seed, had half the PA (0.45 μg/seed) of *R. occidentalis* with a thick, extremely-hard seed coat and diverse sclereids (1.07 μg/seed). PA content and sclereid composition both appear contribute to seed coat hardness and resulting seed dormancy. The effectiveness of sulfuric acid for *Rubus* seed scarification is likely due to degradation of PAs in the testa.

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1. Introduction

Commercially produced *Rubus*, blackberries and raspberries, are vegetatively propagated; however plant breeders use seeds of wild species to introduce new traits and produce improved cultivars. Improving scarification protocols and breaking the deep double dormancy of these seeds requires better knowledge of seed coat structure, thickness and chemical composition.

The seed coat (testa) plays an important role in the plant life cycle by controlling the development of the embryo and determining seed dormancy and germination (Moise et al., 2005). Consequently, seeds with thin or permeable seed coats (or pericarp) lose viability more quickly. The mature seed coat is usually divided into three regions. An exotesta or outer seed-coat layer(s), a mesotesta or middle seed-coat layers(s), and an endotesta or inner seed-coat layer(s); the sclerified tissue of the endocarp can have different origins (Cutler et al., 2007). Thick, sclerified seed coats serve in mechanical protection against physical, chemical and biological damage. Sclerenchyma cells are thick-walled dead cells, variable in size and shape that give rigidity to the plant (Esau, 1977; Metcalfe and Chalk, 1979). Because of their highly variable size and unique shape, sclereids in a plant are often characteristic of the species and could have taxonomic value (Barua and Dutta, 1959). Sclereid types include short, isodiametric brachysclereids (stone cells), elongated rod-like macrosclereids, bone-shaped, columnar osteosclereids, star shaped astrosclereids, long, slender filiform sclereids, and branched trichoschlereids (Blotch, 1946; Nicolson, 1960).

Botanically the fruit of the genus *Rubus* is a drupecetum; an aggregate fruit containing a number of fleshy drupelets attached to a single receptacle. Each drupelet consists of one pyrene; that includes the seed and its surrounding sclerenchymatous endocarp, a fleshy mesocarp and a thin exocarp (Nybom, 1980; Tomlik-Wyremblewska et al., 2010). All *Rubus* seeds are enclosed by hard sclerenchymatous endocarp tissues that impede water imbibition and restrict the oxygen needed for germination (Reeve, 1954; Rose, 1919). Corner (1976) reported that the genus *Rubus* seed is unitegmic with a connate integument and cited Topham (1970)

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