

Explosive Seed Dispersal in Bittercress is due to Juxtaposition of Mucilage and Rigid Cell Types

Kevin C. Vaughn and Andrew J. Bowling*

Southern Weed Science Research Unit, USDA-ARS

*present address: Dow AgroSciences, Indianapolis IN



Abstract

Bittercress (*Cardamine hirsuta*) and mouse ear cress (*Arabidopsis thaliana*) both produce siliques that are morphologically similar to each other: a long cylindrical silique composed of two fused carpels. Despite this external similarity, the bittercress capsules have the ability to discharge their seed explosively, whereas the siliques of mouse ear cress only crack open along the suture lines to disperse their seed. This ability to explosively disperse seed is a competitive advantage to bittercress in propagule dispersal. To determine why these differences occur, we examined the developing seed capsules using microscopic techniques and immunocytochemical probes. Both species organize their siliques similarly. Locules that are filled with seed are surrounded by two carpels connected by a replum that separates the seed cavity into locules. At the interface of the replum and the carpel, a zone of detachment occurs. In the carpels of the bittercress the inner wall (enB layer) of the carpel is highly thickened and enriched in xylans whereas the walls of the mouse ear cress silique are not as thick nor as enriched in xylans. In addition, cells of another layer (enA layer) in the bittercress ovule wall are highly enriched in a mixture of various mucilaginous pectins whereas in the mouse ear cress silique, this layer degenerates before seed dispersal. Both siliques seem to detach at the replum/carpel interface, by the degradation of highly de-esterified pectins in the middle lamellae. However, the tension created by the drying of the mucilaginous cells adjacent to the rigid cells in the bittercress silique creates a pressure that explodes the silique and expels the seed, a force that mouse ear cress silique is unable to generate.

Introduction

Ballistic seed dispersal is one of the more effective ways in which weed seed may be distributed compared to the more passive methods used by many species. Unfortunately, little is known of the mechanisms by which plants propel seed ballistically. In this study, we compare the organization and composition of the siliques of bittercress with the well-studied and closely related mouse ear cress silique that only uses relatively passive methods for dispersal. From these results we suggest a mechanism for ballistic seed dispersal in bittercress based upon a tension created by a drying mucilaginous layer adjacent to a highly thickened tissue.

Material and Methods

Samples of bittercress and mouse ear cress siliques at varying stages of development were fixed and prepared for scanning or light microscopic immunocytochemistry as described in Meloche et al. (2007) and Bowling and Vaughn (2008). Sections were probed with a variety of antibodies that recognize polysaccharide epitopes specific to various classes of polysaccharide, reacted with gold labeled secondary antibody, and intensified with silver as per Meloche et al. (2007). Micrographs were collected digitally from a Zeiss Axioskop.

Results and Discussion

Light microscopic sections (Figure 1) through nearly mature mouse ear cress and bittercress siliques reveal essentially the same internal anatomy. Fused carpels from the exterior of the silique with the seed-bearing chamber (locule) formed from the cavity created by these carpels. The replum runs through the center of the silique and at either end of the replum, a zone of contact between the carpels and the replum will serve as the site of dehiscence. Thus, the basic anatomy of the two siliques is so similar that it is difficult to conceive that such similar structures could behave so differently.

The use of polysaccharide antibodies to these sections reveals both similarities and differences with respect to the composition of the siliques (Figures 2,3). Both species show a reduction highly esterified pectins near the separation zone. Breakdown of the middle lamellae between the small cells in this zone allows for the separation of the carpels from the replum in both species. When the middle lamellae are sufficiently weakened, the carpels separate along this suture line (not shown).

Several differences exist in the carpel walls, however. The innermost layer of the carpel wall, the enA, degenerates in the mouse ear cress silique whereas in the bittercress the enA is retained longer and a large accumulation of mucilaginous pectins accumulates in the space between the enA and enB layers (Figure 3). No mucilage deposits are found in the mouse ear cress. The enB layer is thickened in both species, but in the bittercress the thickening is much more extensive, as are the labeling with antibodies that recognize xylans (Figure 2).

Scanning electron microscopy of the mature mouse ear cress silique reveals seed still enclosed within the carpel even though the silique has split (Figure 4). In contrast, as the bittercress capsule matures, the carpels explode open along the suture, leaving carpels denuded of their seed (Figure 5).

A Model for Explosive Seed Dispersal (Figure 6)

In order to explain the behavior of the bittercress silique, we have devised a model by which two opposing forces work to create the explosive release of the seed. Mucilages such as those found between the enA and enB layers of the carpels are one of the molecules that respond rapidly and markedly with changes in moisture content, in this case as the silique dries that would be changing from a state of maximum hydration (expanded) to maximum dehydration (shrunken). This layer of mucilage is juxtaposed to a layer of highly thickened cell in the enB layer, which because of the thickened walls are going to try to resist the tension created by the shrinking mucilage. As this tension reaches some critical level and the breakdown of the separation zone nears completion, the replum and carpels separate with a violent explosion, hurling the seed up to 15 feet away from the mother plant, ensuring the spread of the species to new habitats.

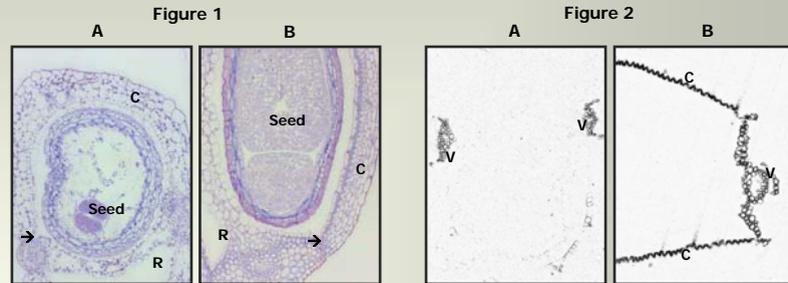


Figure 1

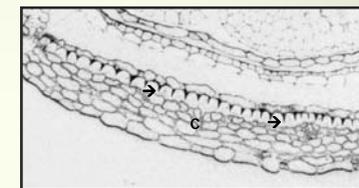


Figure 3

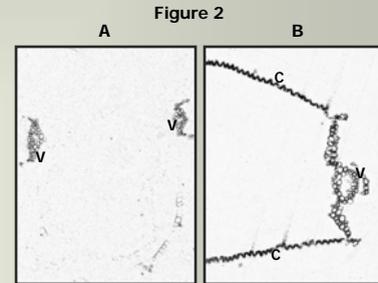


Figure 2

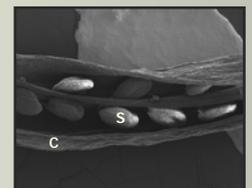


Figure 4

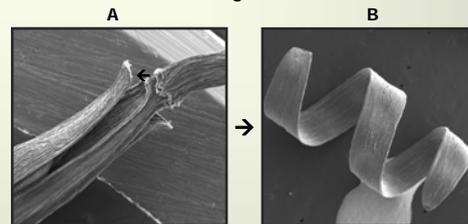


Figure 5

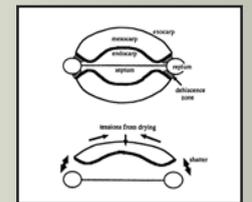


Figure 6

Figure Legends

Figure 1. Light micrographs of mouse ear cress (A) and bittercress (B) siliques. Both species produce siliques in which the carpels (C) form a locule that contains the seed. The replum (R) runs through the middle of the silique and holds the seed. At the interface of the replum and the carpel, the zone of dehiscence (marked with an arrow) occurs.

Figure 2. Serial sections from the block faces shown in Fig 1A were probed with the LM10 antibody that recognize xylans. In the mouse ear cress (A) section, the vascular tissue (V) is labeled and some faint label is found along the carpel. In contrast, in the bittercress silique (B) a layer of highly thickened cells with strong xylan label is in the enB layer of the carpel (C) as well as in the vascular tissue.

Figure 3. Sections of bittercress labeled with antibodies to mucilaginous pectins. A strongly reactive layer of mucilage appears in the interface of the enB and enA cell layers of the carpel (C).

Figure 4. Scanning electron micrograph of the mouse ear cress silique at maturity. Although the seed are not exposed they are not thrown explosively from the capsule. S=seed; C=carpel.

Figure 5. Scanning electron micrographs of bittercress siliques at a stage just before silique explosion (A) and after ballistic seed dispersal (B). In panel A, the very earliest bits of separation between the carpel and the replum can be seen (arrowhead). In panel B, a spiral morphology of the carpel is caused by the relief of tension and the consequent ballistic dispersal of seed.