THE MECHANISM FOR EXPLOSIVE SEED DISPERSAL IN CARDAMINE HIRSUTA (BRASSICACEAE)1

KEVIN C. VAUGHN2,4, ANDREW J. BOWLING2,5, AND KATIA J. RUDEL3

2Crop Production Systems Research Unit, USDA-ARS, P. O. Box 350, Stoneville, Mississippi 38776 USA; and 3Research Center on Plant Macromolecules, CERMAV-CNRS-UPR 5301, BP 41 38041 Grenoble, France

• **Premise:** Although many highly successful weed species use a ballistic seed dispersal mechanism, little is known about the mechanics of this process. Bittercress (Cardamine hirsuta) siliques are morphologically similar to Arabidopsis siliques, but they can project their seeds up to 5 m, while Arabidopsis seeds are dispersed by gravity. Comparison of these species should enable us to determine which structures might be responsible for ballistic seed dispersal.

• **Methods:** Sections of Arabidopsis and bittercress siliques were immunolabeled with antibodies raised against a variety of polysaccharide epitopes.

• **Results:** In bittercress, the second endocarp layer (enB) of the valve had strongly asymmetrical cell wall thickenings, whereas the analogous cells in Arabidopsis were reinforced symmetrically and to a lesser extent. Additionally, an accumulation of mucilaginous pectins was found between the first and second endocarp (enA and enB) layers in the bittercress valve that was not present in Arabidopsis. However, in both species, highly de-esterified homogalacturonan was lost in the dehiscence zone (at the carpel/replum interface) as the siliques matured, thus allowing for separation of the valve at maturity.

• **Conclusions:** Ballistic seed dispersal in bittercress may involve the contraction of the outer pericarp tissue against the highly asymmetrically thickened enB cells, which are hypothesized to bend in one direction preferentially. The stress generated by the differential drying of the inner and outer layers of the valve is released suddenly as the adhesion between the cells of the dehiscence zone is lost, leading to a rapid coiling of the valve and dispersal of the seeds.

**Key words:** Arabidopsis; ballistic seed dispersal; bittercress; Brassicaceae; dehiscence; immunocytochemistry; siliques.

Although plants are often thought of as completely sessile organisms, many aspects of plant life do involve movement (Simons, 1992). For example, circumnutation (Simons, 1992), closing and opening of stomata, righting of tree branches (Bowling and Vaughn, 2008), and coiling of tendrils (Meloche et al., 2007; Vaughn and Bowling, 2009) involve true movement, although even those motions are relatively slow compared to many movement responses in zoological systems. Exceptions to this slower movement are the very rapid release of pollen from bunchberry (Bowling and Vaughn, 2008) and the ballistic dispersal of seeds from capsules such as in Impatiens, Hura, and other species (Simons, 1992). In these cases, the movement is so rapid (0.1 s) that it is difficult to capture these phenomena accurately even with high-speed digital cameras. Movement of anthers of white mulberry has been documented as the fastest biological movement on the planet: half the speed of sound (Taylor et al., 2006). Recently, Skotheim and Mahadevan (2005) described a framework of the scales and speeds of movement that are possible in biological movements. These authors categorized plant movement into three categories: swelling/shrinking, snap buckling, and explosive fracture, with the latter two responsible for the most rapid plant movements. Although this theory explains and classifies some of the mechanics of these movement phenomena, how the plant is able to produce cell types and structures that can accomplish this rapid movement is still largely unknown.

Ballistic seed dispersal is one of the more effective ways in which weed seeds may be distributed compared to the more passive methods used by many species (van der Pijl, 1972; Benvenuti, 2007). For example, jewelweed (Impatiens capensis) may eject seeds as far as 2.0 m from the mother plant, ensuring that its propagules will be spread over a wider area and/ or lessen competition between seedling and the parent plant (Hayashi et al., 2009). In some species, such as bittercress, the ballistic dispersal of seeds serves as an herbivory defense mechanism as well (Yano, 1997). As a potential herbivore encounters a capsule, the touch of the herbivore sets off the dispersal mechanism, springing the insect herbivores far away. Thus, ballistic seed dispersal not only serves as an effective way in which to disperse seed but also to protect them from would-be herbivores.

In this study, siliques of the ballistic species bittercress (also known as hairy bittercress, the common name approved by the Weed Science Society of America) are compared to the much more passive dispersal mechanisms in the siliques of the related and well-studied Arabidopsis siliques (Spence et al., 1996). Selection of mutant silique phenotypes in Arabidopsis has allowed workers to demonstrate the importance of each of the layers in the silique walls in the ability of the silique to open and disperse...
the seeds (Lilegren et al., 2004; Mitsuda and Ohme-Takagi, 2008; Ogawa et al., 2009). Because the silicres of bittercress and Arabidopsis are so similar in every other respect, we were able to draw conclusions as to the nature of cell wall changes that occur during silique development, especially in those characters that were unique to bittercress in allowing for explosive seed dispersal.

**MATERIALS AND METHODS**

**Plant material**—Seeds of bittercress (Cardamine hirsuta L., a generous gift of Ted Whitwell, Horticulture Department, Clemson University, Clemson, South Carolina) were germinated in a soilless potting mix consisting of 3 parts ground pine bark, 3 parts peat and 1 part perlite in a Conviron Growth Chamber (Winnipeg, Manitoba, Canada) under constant illumination. Seedlings were watered with a dilute fertilizer solution. Seeds of Arabidopsis thaliana Columbia strain were obtained originally from Lehole Seeds (Tuscon, Arizona, USA) and were germinated and grown under identical conditions. Siliques of Arabidopsis plants were collected from 9 to 15 d after flowering, which represent a range of development from relatively mature siliques to siliques with seed ready to be dehisced (Louvet et al., 2006). On bittercress plants, three types of siliques were collected: those that could not be stimulated to touch open and occurred just above those that could on the inflorescence, those that could be touch-stimulated to open, and valves from siliques that had naturally opened. These represented similar stages to those observed in the 9–15 d flowering stages of Arabidopsis.

**Microscopy**—Capsules were immersed in 3% (v/v) glutaraldehyde in 0.05 mol/L PIPES buffer (pH 7.4), and pieces of the siliques were excised by cutting with a razor blade in a drop of the fixative on dent wax. The samples were transferred to 20 mL scintillation vials of the same glutaraldehyde solution, and fixation continued for 2 h at room temperature. After this, the samples were washed twice in PIPES buffer at 4°C and fixation continued for 2 h at room temperature. After this, the samples were transferred to 20 mL scintillation vials of the same glutaraldehyde solution, which were washed three times with water and fixed in 1% osmium tetroxide (OSO4) for 1 h, washed three times with water and poststained in uranyl acetate (2 min) and lead citrate (30 s) before observation with a Zeiss EM10CR electron microscope operating at 60 kV. Negatives were scanned with an Epson 700 scanner, and the images were reversed in Photoshop (Adobe, San Jose, California, USA).

**Immunocytochemistry**—Immunogold-silver light microscopy—Groups of sections were removed from the Histofine knife boat with a wire loop to chrome-alum coated slides to which a circle (radius ~1 cm) from a wax pencil was drawn. The sections were dried on a slide warmer and transferred to a slide incubation chamber, and a drop of 1% (w/v) bovine serum albumin (BSA) in 0.02 mol/L phosphate-buffered saline (pH 7.2; PBS) was applied to the slide for 30 min to block nonspecific binding sites. After the blocking stage was over, the solution was decanted and 100 µL of antibody either undiluted or diluted 1:8 in PBS-BSA was added to the ring created by the wax pencil to each slide, and incubation was carried out for 3 h. After the incubation, three exchanges of PBS-BSA were given to each slide, and 100 µL of either goat-antirat or goat anti-mouse IgG coupled to 15-nm gold (EY Laboratories, San Mateo, California, USA) diluted 1:20 in PBS-BSA, 1 h. Grids were then washed extensively in distilled water and poststained in uranyl acetate (2 min) and lead citrate (30 s) before observation with a Zeiss EM10CR electron microscope operating at 60 kV. Negatives were scanned with an Epson 700 scanner, and the images were reversed in Photoshop (Adobe, San Jose, California, USA).

**RESULTS**

**Whole plant descriptions**—Plants of bittercress develop quickly after germination and after ~30 d of growth begin to produce flowers and young siliques, with up to 147 siliques/plant under our conditions. Approximately 10 d after the siliques have started to develop (directly after flowers have shed), they reach a stage where the silique can be triggered to disperse their seeds explosively by touching the silique, even though the seeds are not quite mature at the earliest stages of this ability. Nearly mature siliques, while being examined with a dissecting microscope, often exploded as the light dried the silique ever so slightly, sometimes with just the side toward the light of the dissecting scope dehiscing alone (Fig. 1A). The siliques that explode naturally seem to do this in two different modes. In some, carpels remain attached at the top of the remnant stilar material and coil like a rolltop desk back upon the remnant stilar material (Fig. 1B), whereas other siliques detach completely, leaving a naked stilar remnant (Fig. 1C). These carpels that detach from the replum coil more loosely, similar to a vine. Despite the outward similarity of the siliques of bittercress and Arabidopsis, the bittercress siliques open explosively, resulting in a carpel that is highly coiled after ballistic seed release. In contrast, the carpels of the Arabidopsis siliques remain in an uncoiled position even after the siliques dehisce and after the seeds have been completely dispersed. This only allows for relatively passive seed dispersal in Arabidopsis compared to the bittercress.

**Anatomy of the siliques**—The Arabidopsis siliques have been well described in the literature, and the morphology of the bittercress siliques is very similar to that of Arabidopsis (Fig. 2). When observed in cross section, the two fused carpels form a cavity (locule) in which the seeds reside. The carpels are linked along the central structure called a replum. At either side of the area where the replum is attached to the carpels, a zone of dehiscence occurs where layers of smaller cells occur at the site of silique opening; these are associated with highly thickened cells at either side of the replum (Fig. 2B). In these characteristics of the overall silique organization and dehiscence zone, the siliques of Arabidopsis and bittercress are virtually identical, with the exception of the overall larger dimensions of the bittercress siliques. In the carpels, two internal layers are differentiated from the others. The enB (second endocarp) layer is a layer of highly thickened cells. In the case of Arabidopsis, the thickening are
always occur on the locule side of the wall and the greatest thickening toward the locule as well. The enA cells are the cells innermost in the carpel and are parenchymatous. In the case of the Arabidopsis silique, the enA layer degenerates before silique...
To determine the possible reasons for the differences in silique explosiveness, we probed semithin and thin sections with a battery of antibodies to cell wall constituents. Although all of the antibody localizations that were attempted in these studies are reported in Table 1, here we just describe those antibody localizations relevant to the dispersal.

In both bittercress and *Arabidopsis*, a zone of dehiscence occurs along the site where the carpels and replum meet, and in both species, highly de-esterified homogalacturonans labeled with JIM5 and LM19 are absent or weak in these areas just opening. In bittercress, the cells remain more prominent and a mucilage/polysaccharide aggregation (based upon its similarity in toluidine blue staining with the mucilage in the seed coats) appears to be stored in the intercellular space between the enA layer and the cells of the enB. The staining of the mucilage was variable from section to section and from different areas within the carpel. Even in bittercress, the enA cells appear to be dilated or distorted often bulging into the locule, indicating degeneration or distortion from the tension in the silique even before the seed could be discharged ballistically (Fig. 2C).

**Immunocytchemistry**—To determine the possible reasons for the differences in silique explosiveness, we probed semithin and thin sections with a battery of antibodies to cell wall constituents. Although all of the antibody localizations that were attempted in these studies are reported in Table 1, here we just describe those antibody localizations relevant to the dispersal.

In both bittercress and *Arabidopsis*, a zone of dehiscence occurs along the site where the carpels and replum meet, and in both species, highly de-esterified homogalacturonans labeled with JIM5 and LM19 are absent or weak in these areas just

---

**Fig. 2.** Light microscopic anatomy of the bittercress silique, at a stage just before being able to dehisce naturally. (A) Cross section through the silique material reveals carpels (c) that together with the central replum (r) form a locule where the seed (s) is held. The outer layer of the seed coat has conspicuous mucilage deposits (*). (B) Higher magnification image through the dehiscence zone, showing the interface between the carpel (c) and the replum (r). The actual point of dehiscence is marked by arrowheads at external and internal sides of the silique. At this site, a number of very small cells occur right at the dehiscence site and a layer of thickened cells occurs in the adjoining replum tissue. (C) Section through the carpel layers reveals the distinct endocarp B (enB) layer where the cell walls proximal to the locule are highly thickened in an inverted V-shaped pattern, while the walls on the distal side are not thickened. Large accumulations of mucilage (*) has forced the enA layer cells to loose contact with the enB cells in many cases. Scale bars in (A) = 50 µm; (B and C) = 25 µm.
Table 1. Antibodies used in this study and references to these antibodies.

<table>
<thead>
<tr>
<th>Antibody/antiserum</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>John Innes and Leeds monoclonals</td>
<td></td>
</tr>
<tr>
<td>JIM5</td>
<td>Claussen et al., 2003</td>
</tr>
<tr>
<td>JIM7</td>
<td>Claussen et al., 2003</td>
</tr>
<tr>
<td>JIM8</td>
<td>Knox et al., 1991</td>
</tr>
<tr>
<td>JIM13</td>
<td>Knox et al., 1991</td>
</tr>
<tr>
<td>LM1</td>
<td>Smallwood et al., 1995</td>
</tr>
<tr>
<td>LM5</td>
<td>Jones et al., 1997</td>
</tr>
<tr>
<td>LM6</td>
<td>Willats et al., 1998</td>
</tr>
<tr>
<td>LM10</td>
<td>McCartney et al., 2005</td>
</tr>
<tr>
<td>LM11</td>
<td>McCartney et al., 2005</td>
</tr>
<tr>
<td>LM16</td>
<td>Verherbruggen et al., 2009a</td>
</tr>
<tr>
<td>LM18</td>
<td>Verherbruggen et al., 2009a</td>
</tr>
<tr>
<td>LM19</td>
<td>Verherbruggen et al., 2009a</td>
</tr>
<tr>
<td>LM20</td>
<td>Verherbruggen et al., 2009a</td>
</tr>
<tr>
<td>Complex carbohydrate center monoclonals</td>
<td></td>
</tr>
<tr>
<td>CCRC-M1</td>
<td>Freshour et al., 1996</td>
</tr>
<tr>
<td>CCRC-M7</td>
<td>Freshour et al., 1996</td>
</tr>
<tr>
<td>CCRC-M13</td>
<td>CCRC website a</td>
</tr>
<tr>
<td>CCRC-M22</td>
<td>CCRC website a</td>
</tr>
<tr>
<td>CCRC-M38</td>
<td>W. Willats, personal communication</td>
</tr>
<tr>
<td>Lignin antiserum</td>
<td></td>
</tr>
<tr>
<td>Gzl (G lignin)</td>
<td>Ruel et al., 1994</td>
</tr>
<tr>
<td>G-S lignin</td>
<td>Josseleau and Ruel, 1997</td>
</tr>
<tr>
<td>S lignin</td>
<td>Josseleau et al., 2004</td>
</tr>
</tbody>
</table>

a  CCRC website: http://www.ccrc.uga.edu/~mao/wallmab/Antibodies/antib.htm

Also, the bulk of the Arabidopsis seed coat mucilage does not react with the LM16 antibody (Fig. 5A). In contrast, the bittercress seed coat mucilage seems to be highly enriched in (modified) arabinans (LM16; Fig. 5B), arabinogalactan proteins (AGPs; labeled with JIM13, Fig. 5C; and CCRC-M7; not shown), and RGI recognized by CCRC-M22 (Fig. 5D), that does not label Arabidopsis seed coat mucilage. Some faint label is observed on the bittercress seed coat mucilage with the antihomogalacturonan antibodies, generally bordering the larger accumulation of arabinan/AGP. The columella area of the mucilage cells (the central region where mucilage is not present) is labeled with most of the antibodies that label primary walls in other tissues of the silique. Lignin antisera (G specific as well as S and G-S lignins) also strongly label the outermost portion of the columella region, but not the mucilage itself in these cells.

To examine the relationship between the intercellular mucilage in bittercress more closely, we probed thin sections with the same antibodies used in the light microscopic analysis and examined them via transmission electron microscopy. When sections are labeled with any of the mucilaginous pectin antibodies, the label occurs right up to the highly thickened ends of the enB cells, indicating that the mucilage is tightly associated with the thickened ends of the enB cells, and not the mucilage itself in these cells.

Also, the bulk of the Arabidopsis seed coat mucilage does not react with the LM16 antibody (Fig. 5A). In contrast, the bittercress seed coat mucilage seems to be highly enriched in (modified) arabinans (LM16; Fig. 5B), arabinogalactan proteins (AGPs; labeled with JIM13, Fig. 5C; and CCRC-M7; not shown), and RGI recognized by CCRC-M22 (Fig. 5D), that does not label Arabidopsis seed coat mucilage. Some faint label is observed on the bittercress seed coat mucilage with the antihomogalacturonan antibodies, generally bordering the larger accumulation of arabinan/AGP. The columella area of the mucilage cells (the central region where mucilage is not present) is labeled with most of the antibodies that label primary walls in other tissues of the silique. Lignin antisera (G specific as well as S and G-S lignins) also strongly label the outermost portion of the columella region, but not the mucilage itself in these cells.

**DISCUSSION**

**Similarities and differences between bittercress and Arabidopsis siliques**—One advantage of studying ballistic seed dispersal in the Brassicaceae is having the well-studied and nonballistic Arabidopsis silique as a model because so much is known about the roles of the various tissues in the silique from the investigation of Arabidopsis mutants (e.g., Lilegren et al., 2004; Arsovski et al., 2009). In many respects, the siliques of bittercress and Arabidopsis are very similar. The arrangement of locule, seed, replum, and carpels are virtually identical, save the size of the siliques. In the dehiscence zone, the anatomy is virtually identical, and both species initiate the dehiscence process by the loss of highly de-esterified pectins in the cells of the dehiscence zone. Thus, there are many structures and processes that are quite similar between the two species, despite the radical differences in dispersal mechanisms.

Actually, even in the areas of difference, the differences are still amazingly subtle for such different behaviors in terms of seed dispersal. All of these relate specifically to differences in the carpel, specifically the enA and enB layers. In bittercress, the enA layer persists for a longer time in the development of the capsule, whereas in Arabidopsis the enA layer degenerates rapidly. In the bittercress silique, a large accumulation of mucilaginous pectins occupies the intercellular space between the enA and enB layers. In the Arabidopsis silique, only a weak labeling of homogalacturonans is noted, perhaps residual from the breakdown of the enA layer. Cells in the enB layer of bittercress have a unique pattern of thickenings in an inverted V- or conjoined teardrop-shaped pattern that is present only on the locule side of the enB cells. These thickenings, but not other areas of the enB layer cell wall, are strongly labeled with antibodies to xylan and lignin. The mucilage from the intracellular space is in intimate contact with these wall thickenings. In contrast to the bittercress enB layer, the Arabidopsis enB layer cells are...
thickened, but not to the extent of the bittercress enB cells, and the thickenings are uniform throughout the cell walls (i.e., they are circular in cross section).

**What is the function of the distinctive, V-shaped secondary wall thickenings that run down the length of the cells on the side of the cell closest to the locule in bittercress?**—A linear object with a V-shaped cross section will take much less force to bend toward the open end vs. the spine. Similarly, the cells of the enB layer in bittercress can be predicted to bend much more easily toward the open end of the “V” and away from the apex. In the bittercress, this means that the carpels will bend much more easily to the outside of the siliques than toward the inside. So the role of the thickened cells of the enB layer in bittercress may be 2-fold: one to provide longitudinal stiffness to resist shrinkage and the other to provide a bending direction preference. In contrast, the circular (in cross section) thickenings of enB layer in the Arabidopsis valve would resist bending in any direction. Furthermore, the valve of bittercress is flat, while in Arabidopsis it is cupped (compare the shape of the valves from the two species in Fig. 4A, B). The flat valve of bittercress will allow curling to the outside much more easily than will the cupped valve of Arabidopsis.

**How is the force generated for ballistic seed dispersal in bittercress?**—One possibility is that the bending force is provided by the shrinkage of the mesocarp tissue of the carpel as the silique matures and dries out, like other dehiscent brassicas (Spence et al., 1996). The mesocarp cells of bittercress are not reinforced with lignins or xylan that would prevent or limit their shrinkage upon drying, so as these cells dry, they will tend to shrink and thereby exert a tension on the rigid thickenings of the adjacent enB layer. Furthermore, due to the nearly complete loss of HG that was seen in the dehiscence zone of siliques that had not yet sprung (Fig. 3A, B), these cells would be very easily separated, because this same loss of de-esterified pectins was found to be sufficient for abscission in leaves of Impatiens (Bowling and Vaughn, 2011). The mucilage layer located between the enB and enA layers in bittercress would retain moisture longer than the outer pericarp tissues, so it would prevent

---

**Fig. 3.** Immunocytochemistry with various antihomogalacturonan antibodies of the dehiscence zone region of bittercress. Both (A) JIM5 and (B) LM19 antibodies, which recognize highly de-esterified homogalacturonans (HGs) commonly found in the middle lamellae, reveal a loss of reactivity in the dehiscence zone (between arrowheads). However, (C) JIM7 and (D) CCRC-M38 antibodies, which label HGs with either more highly esterified or a broad range of esterification states, respectively, show no substantial loss of reactivity in this zone. Scale bars = 25 µm.
However, we believe that the tension in the bittercress valve is generated by the contraction of the outer pericarp tissue upon drying, which is more consistent with the general loss of moisture from these organs as they reach maturity, not by drying of the siliques and then rehydration of the inner mucilage layer, as would be required by this model.

Is there a general mechanism for coiled structures?—In other systems in which a curling or coiling motion of a structure is induced, two dramatically different cell types or wall regions are juxtaposed to each other (Witzum and Schulgasser, 1995). One type of wall or wall component is one that changes size with moisture content. This type of wall component is expanded when fully hydrated, but eventually dries and shrinks dramatically upon maturity of the tissue. The second cell type has a highly rigidified cell wall or cell wall layer that resists bending. The drying and shrinkage of the moisture-sensitive cell type/wall

![Fig. 4. Immunocytochemistry of (A) Arabidopsis and (B–D) bittercress siliques. (A) An Arabidopsis silique probed with the LM10 antibody that recognizes xylan. Vascular tissue, thickened cells in the replum (r) and thickened cells in the endocarp B (enB) layer (arrowhead) are labeled. Note that the secondary wall thickenings of the enB layer in Arabidopsis are uniform. (B) Bittercress silique cross section labeled with LM10 reveals a similar labeling pattern to the Arabidopsis siliques, except that secondary wall thickenings of the enB layer (arrowhead) display a characteristic inverted V-shape on the side proximal to the locule. (C) A cross section through the carpel of bittercress reveals the strong labeling of the mucilage (m) between the endocarp A (enA) and enB layers with the JIM5 antibody. (D) A similar section to (C), but probed with the CCRC-M38 antibody reveals similar strong labeling of the mucilage (m). Scale bar in (A, B, D) = 50 µm; (C) = 25 µm.](image-url)
have shown that the average is more like 0.25 m (Bachman and Whitwell, 1994). These differences in the distance of dispersal may reflect differences in silique drying, developmental stages of the parent plant, or seed load within the silique, but such variability would allow for a more balanced spread of seed, both near and more distant from the parent plant. Similar distances of seed dispersal were observed for jewelweed (Hayashi et al., 2009) and in another species of Cardamine. In the case of jewelweed, the plants require relatively moist conditions so that, although the seed would be deposited a good distance from the parent plant, it is also likely that the seed would be deposited on another site with similar favorable growth conditions to what the parent plant was exposed. In fact, bittercress seedlings seem to occur in patches in nursery crops and will solidly fill nursery pots if left uncontrolled. Bittercress seems to occur in more ecological niches than jewelweed, but the ability to move propagules to other close sites has made it a major pest in nurseries and lawns, where it can quickly spread at many favorable sites. In addition, an individual plant may produce up to 5000 seeds (Bachman and Whitwell, 1994) and would quickly make the bittercress plant a formidable weed problem, considering a 

layer puts pressure on the adjoining rigid layer to bend. In the highly coiled pseudo-elaters of hornworts (Carafa et al., 2005; Kremer et al., 2004) and in the G fibers of trees and vines (Meloche et al., 2007; Bowling and Vaughn 2008, 2009), this force is accomplished by a single cell type, with highly hydrated wall layers (containing AGPs or pectins) directly in contact with wall layers that are highly thickened (containing xylans and lignin). As the layers with AGPs or pectins shrink, they put tension on the lignified rigid layers and exert tension. The result is that the cells must change morphology to relieve the tension, and so the characteristic coiled shape of tendrils and pseudoe-laters is generated.

**Advantages to ballistic seed dispersal**—Ballistic seed dispersal offers some obvious advantages, although it might not be what would be most beneficial for some species. Of course, one of the advantages is that the plant does not require any other agent, biotic or abiotic, to enhance seed dispersal. Thus, bittercress seed may be dispersed even in the absence of wind, rain, or animals. Ballistic seed expulsion from bittercress siliques can be as much as 5 m from the parent plant, although other studies have shown that the average is more like 0.25 m (Bachman and Whitwell, 1994). These differences in the distance of dispersal may reflect differences in silique drying, developmental stages of the parent plant, or seed load within the silique, but such variability would allow for a more balanced spread of seed, both near and more distant from the parent plant. Similar distances of seed dispersal were observed for jewelweed (Hayashi et al., 2009) and in another species of Cardamine. In the case of jewelweed, the plants require relatively moist conditions so that, although the seed would be deposited a good distance from the parent plant, it is also likely that the seed would be deposited on another site with similar favorable growth conditions to what the parent plant was exposed. In fact, bittercress seedlings seem to occur in patches in nursery crops and will solidly fill nursery pots if left uncontrolled. Bittercress seems to occur in more ecological niches than jewelweed, but the ability to move propagules to other close sites has made it a major pest in nurseries and lawns, where it can quickly spread at many favorable sites. In addition, an individual plant may produce up to 5000 seeds (Bachman and Whitwell, 1994) and would quickly make the bittercress plant a formidable weed problem, considering a

**Fig. 5.** Seed coat labeling in (A) *Arabidopsis* and (B–D) bittercress seeds with (A, B) the LM16, (C) M22, and (D) JIM13 antibodies. The seed coat muclilage of bittercress is labeled strongly with antibodies that recognize modified arabinans, arabinogalactan proteins (AGPs), and rhamnogalacturonan I (RGI). Bar = 50 µm.
generation can occur in 30–60 d and in favorable climates growth year round. Another major advantage of ballistic seed dispersal is the potential antitherbivory characteristics of these plants. Yano (1997) has shown that caterpillars may be shot several meters from the site of silique explosion. This may be one of the few instances where plants actively fight off the would-be herbivore! Thus, with its combination of large numbers of seeds, quick generation times, year-round growth, and mechanisms to enhance dispersal and discourage predation, bittercress is well poised to be a weed of significance in many situations.

LITERATURE CITED


Fig. 6. Bittercress endocary B (enB) layers probed with (A, C) CCRC-M38 and (B, D) LM10. (A, C) Label with the CCRC-M38 antibody is confined to the mucilage layer (m) although it is contiguous with the highly thickened (t) inverted V-shaped walls of the enB layer. (B, D) LM10 antibody labeling is restricted to the thickened cell wall areas (t) and does not label the mucilage (m). Bar = 1.0 µm.


