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Physiological and molecular aspects of pod shattering resistance in crops

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Abstract: Pod shattering resistance is a trait acquired by crops in the process of evolution. Manipulation of physiological and molecular processes is fundamental for the improvement of shattering resistance in crops. In this review we discuss several enzymes, key hormones and their possible roles or relationships involved in pod shattering, and highlight responsible genes, quantitative traits loci (QTLs) and their implications for increased pod shattering resistance. Cell wall degrading enzymes, particularly β-glucanases and endopolygalacturonases play an important role in the process of pod dehiscence. It is not clear how and to what extent a specific hormone regulates the dehiscence zone differentiation and the dehiscence process is not clear. Resistance to shattering is highly heritable and is not controlled by a single gene. Several QTLs associated to dehiscence have been identified in crops, while the underlying genetic functions of these QTLs deserve further investigation. Further physiological analyses of the pod wall will help to understand better the pod dehiscence.

Keywords: enzymes; gene identification; hormones; QTLs

Crops have been selected for acquired resistance to pod shattering or pod dehiscence to avoid yield losses in the process of domestication (Fuller & Allaby 2009; Bennett *et al*. 2011; Funatsuki *et al*. 2014). Still, susceptibility to pod shattering remains one of major traits resulting in yield losses in many seed crops including soybean (*Glycine max* (L.) Merr.), sesame (*Sesamum indicum* L.), oilseed rape (*Brassica napus* L.), birdsfoot trefoil (*Lotus corniculatus* L.) and other pulse crops (Abd El-Moneim 1993; Grant 1996; Langham & Wiemers 2002; Weeden *et al*. 2002; Child *et al*. 2003; Romkaew *et al*. 2008).

In soybean, the contribution to total yield loss by pod shattering in the South Eastern USA was around 37% (Philbrook & Oplinger 1989), and respective yield loss insusceptible and intermediately susceptible cultivars was 57–175 and 0–186 kg/ha respectively (Tukamuhabwa *et al*. 2002). As much as 40 to 60% shattering rate of matured pods was reported in some common vetch (*Vici sativa* L.) cultivars (Sattell *et al*. 1998; Dong *et al*. 2016). For birdsfoot trefoil, possible yields could be as high as 400 to 600 kg/ha with best management, but as low as 50 kg/ha under poor weather conditions in which seed yield losses by shattering were 3 to 5.3 kg/ha/day (Garcia-Diaz & Steiner 2000; Řepková & Hofbauer 2009). Seed yield losses in big trefoil (*L. uliginosus* Schkuhr.) ranged from 7 to 88% pods with a rate of 10% per

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day due to pod shattering (Hare & Lucas 1984). Yield loss was 11–25% in the pods of many *Brassica* species once they reached maturity (Price *et al*. 1996), and up to 50% in adverse seasons (MacLeod 1981). Besides the economic importance from the yield loss, pod shattering can also lead to the emergence of volunteer weeds in the subsequent growing season, thus impeding future crop rotations. Differences in pod anatomy and morphology in soybean may cause pod dehiscence (Zhang *et al*. 2018), while the physiological and molecular nature factors are pivotal for the improvement of shattering resistance in crops. This paper intends to discuss an overview of the control of pod dehiscence from the aspects of enzymes, phytohormones, genes and QTLs participation and functioning, with an aim to provide insight and further understanding of the pod dehiscence mechanism and to devise strategies in manipulating and reducing the problem.

Enzymes involved in pod shattering process

Dehiscence zone (DZ) is the element involved in pod dehiscence (Ferrándiz 2002).The pod shattering and seed release are mostly due to the loss of cellular cohesion and degradation of the middle lamella in DZ (Carlson & Lersten 2004; Bennett *et al*. 2011). The degradation of pectin, especially homogalacturonan-rich pectin in the middle lamella has been commonly found in fruit shattering, and pectin integrity is suggested to be important for cell adhesion (Ridley *et al*. 2001; Dong & Wang 2015).

An increased β-glucanase activity in the cells of the DZ and accompanied degradation of the cell wall at the site of fruit dehiscence, were found in *Brassica* (Kemmerer & Tucker 1994). Result with antibodies againstβ-glucanase indicated that the break strength in the abscission zone was significantly reduced by antibodies injection, while the changes of this enzyme and its distribution were completely involved in abscission processes, indicating that β-glucanase is actually required for abscission (Sexton *et al.*1980).

Endopolygalacturonase (endo-PG) termed RD-PG1e, specifically expressed in the DZ, catalyzes the main chain of the homogalacturonan region of pectin, i.e. the hydrolysis of α-1,4-glycosidic bonds in polygalacturonic acid. This hydrolysis process was considered to facilitate the breakdown of the middle lamella (Christiansen *et al*. 2002). The endo-PG transcript analysis in soybean further indicated that the endo-PG was involved in the breakdown of the middle lamella before the occurrence of dehiscence, and thus played an active role in the process of pod shattering. β-glucuronidase (GUS) staining of the transgenic Arabidopsis lines and inhibited formation of abscission layers without PG all demonstrated and supported this idea (Ogawa *et al*. 2009).

Although no correlation was observed between pod dehiscence and the PG activity either temporally or spatially (Meakin & Roberts 1990), and very few direct genetic evidence was found for the physiological importance of individual PGs, there was a report showing that increasing PG activity was correlated with cell separation in the shedding of fruit (Kalaitzis *et al.* 1997). The increased activities of endo-1,4-β-glucanases and endo-PG, but a significant decrease of the protein content in the DZ throughout maturation and senescence were also found (Christiansen *et al*. 2002). These findings indicated that endo-1,4-glucanases and endo-PG may disintegrate the middle lamella in the separation layer, and the outcome is a decreased cell to cell adhesion.

Therefore, cell wall-modifying enzymes affect the breakdown of DZ, which should be closely involved in the processes of pod dehiscence through cell wall disassembly, reconstruction and adjacent cell bindings required for dehisced pods (Hadfield *et al*. 1998; del Campillo 1999; Rose & Bennett 1999). Further examination of their expression and activity in the pod tissues and/or contributions to the breakdown of the cell wall is required.

Hormones in pod shattering

As a biologically active and readily diffusible phytohormone, ethylene has been identified in association with the processes of fruit ripening and abscission (Abeles *et al*. 1992). The onset of pod dehiscence was correlated with a burst in seed ethylene production, and a transient peak production of ethylene was also temporally correlated with the increase in β-glucanase activity, the enzyme responsible for the degradation of the cell wall leading to shattering (Oeller *et al*. 1991). It should be noted that exposure to the gas does not accelerate pod shattering while the peak in ethylene production might only act as a signal factor for pod dehiscence since the climax usually precedes dehiscence. Actually, the fleshy and dehiscent fruits become more competent in response to ethylene ripening signals as they age (Joaquin *et al*. 2007). Therefore, peak production of the ethylene might be only responsible for the acceleration of the senescence onset but not dehiscence promotion (John *et al*. 1995).

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In the abscission zone, the inhibition of β-1,4-glucanase mRNA accumulation by auxin has been reported, and the decreased auxin content in the DZ was correlated with increased β-glucanase activity (Tucker *et al.*1988). Pods treated with 4-CPA (auxin mimic 2-methy l-4-chlorophenoxyacetic acid) delayed β-1,4-glucanase activity approximately 10 d and concomitant cell separation in the DZ (Chauvaux *et al*. 1997). Dehiscence zone differentiation required auxin accumulation in early stages, while auxin depletion at later stages could be important for triggering cell separation (Ballester & Ferrándiz 2017). These findings suggest that the regulation of auxin and its concentrations on pod dehiscence is partially associated to the activation of the β-1,4-glucanase activity in the DZ.

Gibberellic acid (GA) was shown to be important for the continued pod elongation in oil seed rape (Bouttier & Morgan 1992) and is completely required, for the correct functioning of INDEHISCENT protein in Arabidopsis fruit (Arnaud *et al*. 2010). However, functions of GA on pod dehiscence have not been fully examined. Furthermore, less research has been conducted on the involvement of the two phytohormones, abscisic acid and cytokinins on pod dehiscence in crops, although their roles in other aspects of plant development have been highlighted (Finkelstein 2013; Humplik *et al.* 2017).

Therefore, how and to what extent a specific hormone regulates DZ differentiation and the dehiscence process is not clear. Since phytohormones could change during pod development, and can either act synergistically or antagonistically towards one other, it is possible that not a single hormone but phytohormones interactions are actively involved in pod shattering. Changes of individual hormone during pod development particularly hormone balance or interplay in relation to pod dehiscence need to be fully identified, which may add more knowledge and shed insight for their roles in pod and seed development.

Genes involved in pod dehiscence

In soybean, the first gene, *Pdh1* (*Pod Dehiscence1*), was identified as a candidate for leading protein involved in pod dehiscence (Ralph *et al*. 2007; Funatsuki *et al*. 2008). This gene is highly expressed in the lignin-rich inner sclerenchyma of pod walls at the stage of initiation in lignin deposition, which promotes pod dehiscence by increasing the torsion of dried pod walls, and thus serves as a driving force for pod dehiscence (Funatsuki *et al*. 2014).

Another gene, NAC (The NAM, ATAF1/2 and CUC2 domain protein) *SHATTERING1-5* (*SHAT1-5*) activates secondary wall biosynthesis and enhances pod-wall binding strength through the thickening of fibre cap cells in secondary walls of the pod ventral suture (Dong *et al*. 2014). In *Arabidopsis*, evidences indicated that a subset of closely related NAC domain proteins, including NST1/ANAC043, NST2/ANAC066, and NST3/SND1(Secondary Wall-associated NAC Domain Protein)/ANAC012 act as master transcriptional switches governing secondary cell wall biosynthesis in a partially redundant manner (Mitsuda *et al*. 2005; Zhong *et al*. 2007).

A recessive allele was responsible for non-shattering characteristics in wild types of common vetch, whereas dominant alleles were identified for shattering in cultivated types (Abd El-Moneim 1993). In pea, a main candidate gene for pod dehiscence was localized on LGIII, and identified as proline-rich extensin-like protein or a homolog of peptidoglycan-binding domain protein (PGDB) of *Medicago truncatula* (Tayeh *et al*. 2015). As extensins are structural cell-wall proteins specific to plants, and can substantially regulate mechanical cell wall properties through linkages to other cell wall component (Lamport *et al*. 2011). The *MACE-P015* gene is supposed to have a general peptidoglycan binding function and thought to play a critical role in pod dehiscence of pea. In *Arabidopsis thaliana*, not only *SHATERPROOF1* and *SHATERPROOF2* genes dominantly regulate DZ formation, but are also two partially redundant genes that control the formation of secondary cell walls of pods (Liljegren *et al*. 2000; Dinneny & Yanofsky 2005; Mitsuda & Ohme-Takagi 2008). This suggested that multiple genes with minor effects fundamentally determine the resistance to pod shattering in crops (Liu *et al.* 2007).

Therefore, genes as the main regulators of lignified layer establishment in pod wall development, cause pod dehiscence. Since current literature shows that it is not a single candidate gene underlying pod dehiscence for any crop, the identification and differentiation of homologous or novel genes defining dehiscence zone from the pod suture as well as venture tissue are still a great challenge in understanding the molecular mechanism of the pod dehiscence resistance in crops.

QTL involved in pod dehiscence

Common quantitative trait loci (QTLs) related to shattering resistance have already been identified from several crops (Paterson 2001). A single locus

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controlling pod dehiscence (PD) was found in lentil, while two loci, one controlled the number of twists along the length of the shattered pod, and the other one controlled the percentage of shattered pods, were identified in mung bean (Isemura *et al*. 2007). Two similar loci were found in pea (Weeden *et al*. 2002; Weeden 2007), and common bean (Koinange *et al*. 1996). *Dpo* locus responsible for loss of PD in pea was localized on LGIII (Bordat *et al*. 2011).

Considerable progress has been achieved in QTL identification in soybean. Restriction fragment length polymorphism (RFLP) loci linked to QTL conditioning resistance to PD in soybean were identified in 1997. The consistency of QTL across locations indicated that PD was highly heritable and conditioned by one major and a few minor QTLs. Their findings provided a basis for comparative mapping of the trait in other legumes. QTL for *Pod Dehiscence1* (*qPDH1*) was the major QTL controlling pod dehiscence in soybean (Bailey *et al*. 1997), which most likely affected the process of lignin biosynthesis or composition of the lignified cell walls (Suzuki *et al.* 2009). This QTL was found to be located between simple sequence repeat markers, Sat_093 andSat_366, and the shattering resistance allele at *qPDH1* was proved to be valuable in different genetic backgrounds at multiple locations (Funatsuki *et al*. 2008). However, *pdh1* for the shattering-resistant genotype is defective because it has a premature stop codon (Funatsuki *et al*. 2014).

Three QTLs, two on LG J and one on LG D1b were found, while QTLs on LG J were mapped quite far away from *qPDH1* (Saxe *et al*. 1996). A QTL, identical to *qPDH1*was also detected on LG J in another study, however, its effect was not big enough (Liu *et al*. 2007). No major QTL but only a minor QTL only was detected either on LG J, or on other LGs in the segregating population of soybean derived from a shattering susceptible cultivar, and a shattering resistant cultivar (Kang *et al*. 2009). These findings suggest that (1) other identified QTLs are likely to differ from *qPDH*; (2) multiple alleles at *qPDH1* or other QTLs near *qPDH1*existed for pod dehiscence; and (3) a shattering resistant cultivar might be developed by pyramiding shattering resistance alleles at minor QTL. Fine mapping and identification of QTLs with large effects on pod dehiscence specific to soybean or legumes deserve further investigation.

Concluding remarks

Cell wall degrading enzymes, particularly β-glucanases and endopolygalacturonases play an important role in the process of pod dehiscence. How and to what extent a specific hormone regulates DZ differentiation and the dehiscence process is not clear. Interactions among phytohormones might be more important than a single hormone in DZ differentiation and/or as triggers of pod shattering. Shattering resistance is highly heritable and is not controlled by one gene. Several QTLs associated with dehiscence have been identified in legume crops, but the identification of the underlying genetic functions lags far behind. The understanding of how pods 'unzip' at molecular level is essentially important, which could provide a further avenue for regulating pod dehiscence. Further physiological analyses of pod tissues, particularly those of the pod wall will assist in the fully understanding pod dehiscence. Plant biologists and breeders are still confronted with a great challenge in manipulating or tackling the forefront of the pod dehiscence issue.

References

Abd El-Moneim A.M. (1993): Selection for non-shattering common vetch, *Vicia sativa* L. Plant Breeding, 110: 168–171.

Abeles F., Morgan P., Saltveit M. (1992): Ethylene in Plant Biology. San Diego, Academic Press.

Arnaud N., Girin T., Sorefan K., Fuentes S., Wood T.A., Lawrenson T., Sablowski R., Østergaard L. (2010): Gibberellins control fruit patterning in *Arabidopsis thaliana*. Genes & Development, 24: 2127–2132.

Bailey M.A., Mian M.A.R., Carter Jr. T.E., Ashley D.A., Boerma H.R. (1997): Pod dehiscence of soybean: identification of quantitative trait loci. Journal of Heredity, 88: 152–154.

Ballester P., Ferrándiz C. (2017): Shattering fruits: variations on a dehiscent theme. Current Opinion in Plant Biology, 35: 68–75.

Bennett E.J., Roberts J.A., Wagstaff C. (2011): The role of the pod in seed development: strategies for manipulating yield. New Phytologist, 190: 838–853.

Bordat A., Savois V., Nicolas M., Salse J., Chauveau A., Bourgeois M., Potier J., Houtin H., Rond C., Murat F., Marget P., Aubert G., Burstin J. (2011): Translational genomics in legumes allowed placing in silico 5460 unigenes on the pea functional map and identified candidate genes in *Pisum sativum* L. G3: Genes Genomes Genetics, 1: 93–103.

Bouttier C., Morgan D.G. (1992): Development of oilseed rape buds, flowers and pods *in vitro*. Journal of Experimental Botany, 43: 474–493.

https://doi.org/10.17221/104/2018-CJGPB

Carlson J.B., Lersten N.R. (2004): Reproductive morphology. In: Boema H.R., Specht J.E. (eds.): Soybeans: Improvement, Production, and Uses, Agronomy. No. 16, 3rd Ed., Madison, American Society of Agronomy-Crop Science Society of America-Soil Science Society of America: 59–95.

Chauvaux N., Child R., John K., Ulvskov P., Borkhardt B., Prinsen E., Van Onckelen H.A. (1997): The role of auxin in cell separation in the dehiscence zone of oilseed rape pods. Journal of Experimental Botany, 48: 1423–1429.

Child R.D., Summers J.E., Babij J., Farrent J.W., Bruce D.M. (2003): Increased resistance to pod shatter is associated with changes in the vascular structure in pods of resynthesized *Brassica napus* line. Journal of Experimental Botany, 54: 1919–1930.

Christiansen L.C., Dal Degan F., Ulvskov P., Borkhardt B. (2002): Examination of the dehiscence zone in soybean pods and isolation of a dehiscence-related endopolygalacturonase gene. Plant, Cell & Environment, 25: 479–490.

del Campillo E. (1999): Multiple endo-1,4-beta-D-glucanase (cellulase) genes in *Arabidopsis*. Current Topics in Developmental Biology, 46: 39–61.

Dinneny J.R., Yanofsky M.F. (2005): Drawing lines and borders: how the dehiscent fruit of *Arabidopsis* is patterned. Bioessays, 27: 42–49.

Dong Y., Wang Y.Z. (2015): Seed shattering: from models to crops. Frontiers in Plant Science, 6: 476.

Dong Y., Yang X., Liu J., Wang B.H., Liu B.L., Wang Y.Z. (2014): Pod shattering resistance associated with domestication is mediated by a *NAC* gene in soybean. Nature Communications, 5: 3352.

Dong D.K., Dong R., Wang Y.R., Nie B., Liu Z.P. (2016): The study on pod development and ventral suture structure of *Vicia sativa* cultivar Lanjian No. 3. Acta Botanica Boreali-Occidentalia Sinica, 36: 1376–1382. (in Chinese with English abstract)

Ferrándiz C. (2002): Regulation of fruit dehiscence in *Arabidopsis*. Journal of Experimental Botany, 53: 2031–2038.

Finkelstein R. (2013): Abscisic acid synthesis and response. Arabidopsis Book, 11: e0166.

Fuller D.Q., Allaby R.G. (2009): Seed dispersal and crop domestication: shattering, germination and seasonality in evolution under cultivation. In: Østergaard L. (ed.): Annual Plant Reviews, Volume 38: Fruit Development and Seed Dispersal, Wiley: 238–295.

Funatsuki H., Hajika M., Hagihara S., Yamada T., Tanaka Y., Tsuji H., Ishimoto M., Fujino K. (2008): Confirmation of the location and the effects of a major QTL controlling pod dehiscence in soybean, qPDH1, in soybean. Breeding Science, 58: 63–69.

Funatsuki H., Suzuki M., Hirose A., Inaba H., Yamada T., Hajika M., Komatsu K., Katayama T., Sayama T., Ishimoto M. (2014): Molecular basis of a shattering resistance boosting global dissemination of soybean. Proceedings of National Academy of Science USA, 111: 17797–17802.

Garcia-Diaz C.A., Steiner J.J. (2000): Birdsfoot trefoil seed production: III. Seed shatter and optimal harvest time. Crop Science, 40: 457–462.

Grant W.F. (1996): Seed pod shattering in the genus *Lotus* (Fabaceae): a synthesis of diverse evidence. Canadian Journal of Plant Science, 76: 447–456.

Hadfield K.A., Rose J.K.C., Yaver D.S., Berka R.M., Bennett A.B. (1998): Polygalacturonase gene expression in ripe melon fruit supports a role for polygalacturonase in ripening associated pectin disassembly. Plant Physiology, 117: 363–373.

Hare M.D., Lucas. R.J. (1984): "Grasslands Maku" lotus seed production. Development of Maku lotus seed and the determination of time of harvest for maximum seed yields. Journal of Applied Seed Production, 2: 58–64.

Humplik J.F., Bergougnoux V., Van Volkenburgh E. (2017): To stimulate or inhibit? That is the question for the function of abscisic acid. Trends in Plant Science, 22: 830–841.

Isemura T., Kaga A., Konishi S., Ando T., Tomooka N., Han O.K., Vaughan D.A. (2007): Genome dissection of traits related to domestication in azuki bean (*Vigna angularis*) and comparison with other warm-season legumes. Annals of Botany, 100: 1053–1071.

Joaquin T.B.M., Trejo C., Hernandez-Garay A., Perez P.J., Garcia A.D.G., Quero C.A.R. (2007): Effects of ethephon, salicylic acid and cidef-4 on the yield and quality of guinea grass seed. Tropical Grasslands, 41: 55–60.

John I., Drake R., Farrell A., Cooper W., Lee P., Horton P., Grierson D. (1995): Delayed leaf senescence in ethylene deficient ACC-oxidase antisense tomato plants-molecular and physiological analysis. Plant Journal, 7: 483–490.

Kalaitzis P., Solomos T., Tucker M.L. (1997): Three different polygalacturonases are expressed in tomato leaf and flower abscission, each with a different temporal expression pattern. Plant Physiology, 113: 1303–1308.

Kang S.T., Kwak M., Kim H.K., Choung M.G., Han W.Y., Baek I.Y., Kim M.Y., Van K., Lee S.H. (2009): Population-specific QTLs and their different epistatic interactions for pod dehiscence in soybean [*Glycine max* (L.) Merr.]. Euphytica, 166: 15–24.

Kemmerer E.C., Tucker M.L. (1994): Comparative study of cellulases associated with adventitious root initiation, apical buds, and leaf, flower, and pod abscission zones in soybean. Plant Physiology, 104: 557–562.

Koinange E.M.K., Singh S.P., Gepts P. (1996): Genetic control of the domestication syndrome in common bean. Crop Science, 36: 1037–1045.

Langham D.R., Wiemers T. (2002): Progress in mechanizing sesame in the US through breeding. In: Janic J.,

https://doi.org/10.17221/104/2018-CJGPB

Whipkey A. (eds.): Trends in New Crops and New Uses. Alexandria, ASHS Press: 157–173.

Lamport D.T.A., Kieliszewski M.J., Chen Y.N., Cannon M.C. (2011): Role of the extensin superfamily in primary cell wall architecture. Plant Physiology, 156: 11–19.

Liljegren S.J., Ditta G.S., Eshed H.Y., Savidge B., Bowman J.L., Yanofsky M.F. (2000): *SHATTERPROOF* MADS-box genes control seed dispersal in *Arabidopsis*. Nature, 404: 766–770.

Liu B., Fujita T., Yan Z.H., Sakamoto S., Xu D., Abe J. (2007): QTL mapping of domestication-related traits in soybean (*Glycine max*). Annals of Botany, 100: 1027–1038.

MacLeod J. (1981): Harvesting in Oilseed Rape. Cambridge Agricultural Publishing, London: 107–120.

Meakin P.J., Roberts J.A. (1990): Dehiscence of fruit in oilseed rape (*Brassica napus* L.). II. The role of cell wall degrading enzymes and ethylene. Journal of Experimental Botany, 41: 1003–1011.

Mitsuda N., Ohme-Takagi M. (2008): NAC transcription factors NST1 and NST3 regulate pod shattering in a partially redundant manner by promoting secondary wall formation after the establishment of tissue identity. Plant Journal, 56: 768–778.

Mitsuda N., Seki M., Shinozaki K., Ohme-Takagi M. (2005): The NAC transcription factors NST1 and NST2 of *Arabidopsis* regulate secondary wall thickenings and are required for anther dehiscence. Plant Cell, 17: 2993–3006.

Oeller P.W., Min-Wong L., Taylor L.P., Pike D.A., Athanasios T. (1991): Reversible inhibition of tomato antisense RNA. Science, 437: 5–7.

Ogawa M., Kay P., Wilson S., Swain S.M. (2009): ARABIDOPSIS DEHISCENCE ZONE POLYGALACTURONASE1 (ADPG1), ADPG2, and QUARTET2 are polygalacturonases required for cell separation during reproductive development in *Arabidopsis*. The Plant Cell, 21: 216–233.

Patterson S.E. (2001): Cutting loose. Abscission and dehiscence in *Arabidopsis*. Plant Physiology, 126: 494–500.

Philbrook B., Oplinger E.S. (1989): Soybean field losses as influenced by harvest delays. Agronomy Journal, 81: 251–258.

Price J.S., Neale M.A., Hobson R.N., Bruce D.M. (1996): Seed losses in commercial harvesting of oilseed rape. Journal of Agricultural Engineering Research, 80: 343–350.

Ralph S.G., Jancsik S., Bohlmann J. (2007): Dirigent proteins in conifer defense II: Extended gene discovery, phylogeny, and constitutive and stress-induced gene expression in spruce (*Picea* spp.). Phytochemistry, 68: 1975–1991.

Řepkova J., Hofbauer J. (2009): Seed pod shattering in the genus *Lotus* and its overcoming. Czech Journal of Genetics and Plant Breeding, 45: 39–44.

Ridley B.L., O'Neill M.A., Mohnen D. (2001): Pectins: Structure, biosynthesis, and oligogalacturonide-related signaling. Phytochemistry, 57: 929–967.

Romkaew J., Nagaya Y., Goto M., Suzuki K., Umezaki T. (2008): Pod dehiscence in relation to chemical components of pod shell in soybean. Plant Production Science, 11: 278–282.

Rose J.K., Bennett A.B. (1999): Cooperative disassembly of the cellulose-xyloglucan network of plant cell walls: parallels between cell expansion and fruit ripening. Trends in Plant Science, 4: 176–183.

Sattell R., Dick R., Luna J., Peachey R.E. (1998): Common Vetch (*Vicia sativa* L.). Corvalis, Corvallis Extension Service, Oregon State University.

Saxe L.A., Clar C., Li S.F., Lumpki T.A (1996): Mapping the pod shattering trait in soybean. Soybean Genetics Newsletter, 23: 250–253.

Sexton R., Durbin M.L., Lewis L.N., Thomson W.W. (1980): Use of cellulase antibodies to study leaf abscission. Nature, 283: 873–874.

Suzuki M., Fujino K., Funatsuki H. (2009): A major soybean QTL, *qPDH1*, controls pod dehiscence without marked morphological change. Plant Production Science, 12: 217–223.

Tayeh N., Klein A., LePaslier M.-C., Jacquin F., Houtin H., Rond C., Chabert-Martinello M., Magnin-Robert J.-B., Marget P., Aubert G., Burstin J. (2015): Genomic prediction in pea: Effect of marker density and training population size and composition on prediction accuracy. Frontiers in Plant Science, 6: 1–10.

Tucker M.L., Sexton R., Del Campillo E., Lewis L.N. (1988): Bean abscission cellulose: Characterization of a cDNA clone and regulation of gene expression by ethylene and auxin. Plant Physiology, 88: 1257–1262.

Tukamuhabwa P., Dashiell K.E., Rubaihayo P., Nabasirye M. (2002): Determination of field yield loss and effect of environment on pod shattering in soybean. African Crop Science Journal, 10: 203–209.

Weeden N.F. (2007): Genetic changes accompanying the domestication of *Pisum sativum*: Is there a common genetic basis to the 'domestication syndrome' for legumes? Annals of Botany, 100: 1017–1025.

Weeden N.F., Brauner S., Przyborowski J.A. (2002): Genetic analysis of pod dehiscence in pea (*Pisum sativum* L.). Cellular & Molecular Biology Letters, 7: 657–663.

Zhang Q.Y., Tu B.J., Liu C.K., Liu X.B. (2018): Pod anatomy, morphology and dehiscing forces in pod dehiscence of crops. Flora, 248: 48–53.

Zhong R., Richardson E.A., Ye Z.H. (2007): Two NAC domain transcription factors, SND1 and NST1, function redundantly in regulation of secondary wall synthesis in fibers of Arabidopsis. Planta, 225: 1603–1611.

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