

UNRAVELING THE DYNAMICS OF SEED LONGEVITY: FROM DORMANCY TO GERMINATION

G. CHEBOTAR, A. BÖRNER

Leibniz Institute of Plant Genetics and Crop Plant Research, 06466 Seeland, OT Gatersleben, Germany

Address for correspondence: Chebotar G.,

e-mail: chebotar@ipk-gatersleben.de

The article's aims are to be a comprehensive exploration of factors influencing seed longevity, emphasizing the importance of seed viability for future plant generations, biodiversity conservation, and agricultural productivity. It covers topics related to seed biology, storage conditions, the impact of reactive oxygen species (ROS) and reactive nitrogen species (RNS), the role of seed-associated microbiomes, DNA damage, genetic factors affecting longevity, and the intricate processes involved in seed germination. The discrepancies between artificially aged seeds and those aged naturally in ambient and long-term genebank conditions are discussed, underlining the importance of studying long-term stored seeds to identify genetic markers associated with seed longevity accurately and highlighting the application of genome-wide association studies (GWAS) in uncovering genetic factors.

Key words: longevity, seeds, artificial and natural aging.

РОЗКРИТТЯ ДИНАМІКИ ДОВГОВІЧНОСТІ НАСІННЯ: ВІД СТАНУ СПОКОЮ ДО ПРОРОСТАННЯ

Метою статті є всебічне дослідження факторів, що впливають на довговічність насіння, з акцентом на важливості життєздатності насіння для майбутніх поколінь рослин, збереження біорізноманіття та продуктивності сільського господарства. У ній розглядаються теми, пов'язані з біологією насіння, умовами зберігання, впливом активних форм кисню (ROS) та активних форм азоту (RNS), роллю мікробіомів, пов'язаних із насінням, пошкодженням ДНК, генетичними факторами, що впливають на довговічність, та складними процесами, що відбуваються під час проростання насіння. Обговорюються розбіжності між штучно зістареним насінням та тим, що природно старіє в умовах навколишнього середовища та довгострокового зберігання в генних банках, підкреслюючи важливість вивчення насіння, що зберігається впродовж тривалого часу, для точної ідентифікації генетичних

маркерів, пов'язаних із довговічністю насіння, та висвітлення застосування повногеномних асоціативних досліджень (GWAS) для виявлення генетичних факторів.

Ключові слова: довговічність, насіння, штучно викликане й природне старіння.

REFERENCES

- Agacka-Mołodoch, M., Arif, M.A., Lohwasser, U., Doroszewska, T., Qualset, C.O., Börner, A., The inheritance of wheat grain longevity: a comparison between induced and natural ageing, *J. Appl. Genet.*, 2016, vol. 57, no. 4, pp. 477–481. <https://doi.org/10.1007/s13353-016-0348-3>
- Ariel, F., Jegu, T., Latrasse, D., Romero-Barrios, N., Christ, A., Benhamed, M., Crespi, M., Noncoding transcription by alternative RNA polymerases dynamically regulates an auxin-driven chromatin loop, *Mol. Cell*, 2014, vol. 55, no. 3, pp. 383–396. <https://doi.org/10.1016/j.molcel.2014.06.011>
- Arif, M.A.R., Afzal, I., Börner, A., Genetic aspects and molecular causes of seed longevity in plants, *Plants (Basel)*, 2022, vol. 11, no. 5, 598. <https://doi.org/10.3390/plants11050598>
- Arif, M.A.R., Börner, A., Mapping of QTL associated with seed longevity in durum wheat (*Triticum durum* Desf.), *J. Appl. Genet.*, 2019, vol. 60, pp. 33–36. <https://doi.org/10.1007/s13353-018-0477-y>
- Arif, M.A.R., Börner, A., An SNP based GWAS analysis of seed longevity in wheat, *Cereal Res. Commun.*, 2020, vol. 48, pp. 149–156. <https://doi.org/10.1007/s42976-020-00025-0>
- Arif, M.A.R., Agacka-Mołodoch, M., Qualset, C.O., Börner, A., Mapping of additive and epistatic QTLs linked to seed longevity in bread wheat (*Triticum aestivum* L.), *Cereal Res. Commun.*, 2022. <https://doi.org/10.1007/s42976-021-00240-3>
- Bailly, C., El-Maarouf-Bouteau, H., Corbineau, F., From intracellular signaling networks to cell death: the dual role of reactive oxygen species in seed physiology, *C. R. Biol.*, 2008, vol. 331, no. 10, pp. 806–814. <https://doi.org/10.1016/j.crvi.2008.07.022>
- Ballesteros, D., Pritchard, H.W., Walters, C., Dry architecture: towards the understanding of the variation of longevity in desiccation-tolerant germplasm, *Seed Sci. Res.*, 2020, vol. 30, pp. 142–155. <https://doi.org/10.1017/S0960258520000239>
- Bentsink, L., Alonso-Blanco, C., Vreugdenhil, D., Tesnier, K., Groot, S.P., Koornneef, M., Genetic analysis of seed-soluble oligosaccharides in relation to seed storability of Arabidopsis, *Plant Physiol.*, 2000, vol. 124, no. 4, pp. 1595–1604. <https://doi.org/10.1104/pp.124.4.1595>
- Berrios, L., Rentsch, J.D., Linking reactive oxygen spe-

- cies (ROS) to abiotic and biotic feedbacks in plant microbiomes: The dose makes the poison, *Int. J. Mol. Sci.*, 2022, vol. 23, no. 8, 4402. <https://doi.org/10.3390/ijms23084402>
- Bewley, J.D., Seed germination and dormancy, *The Plant Cell*, 1997, vol. 9, no. 7, pp. 1055–1066. <https://doi.org/10.1105/tpc.9.7.1055>
- Bewley, J.D., Breaking down the walls – a role for endo- β -mannanase in release from seed dormancy?, *Trends Plant Sci.*, 1997, vol. 2, pp. 464–469. [https://doi.org/10.1016/S1360-1385\(97\)01147-3](https://doi.org/10.1016/S1360-1385(97)01147-3)
- Bove, J., Jullien, M., Grappin, P., Functional genomics in the study of seed germination, *Genome Biol.*, 2002, vol. 3. <https://doi.org/10.1186/gb-2001-3-1-reviews1002>
- Bueso, E., Ibáñez, C., Sayas, E., Mucoz-Bertomeu, J., Gonzalez-Guzman, M., Rodriguez, P.L., Serrano, R., A forward genetic approach in *Arabidopsis thaliana* identifies a RING-type ubiquitin ligase as a novel determinant of seed longevity, *Plant Sci.*, 2014, vol. 215, pp. 110–116. <https://doi.org/10.1016/j.plantsci.2013.11.004>
- Bueso, E., Mucoz-Bertomeu, J., Campos, F., Brunaud, V., Martínez, L., Sayas, E., Ballester, P., Yenush, L., Serrano, R., ARABIDOPSIS THALIANA HOMEBOX25 uncovers a role for gibberellins in seed longevity, *Plant Physiol.*, 2014, vol. 164, pp. 999–1010. <https://doi.org/10.1104/pp.113.232223>
- Carrera-Castaco, G., Calleja-Cabrera, J., Pernas, M., Gyme, L., Ocate-Sánchez, L., An updated overview on the regulation of seed germination, *Plants (Basel)*, 2020, vol. 9, no. 6, p. 703. <https://doi.org/10.3390/plants9060703>
- Carrillo-Barral, N., Rodríguez-Gacio, M.D.C., Matilla, A.J., Delay of Germination-1 (DOG1): a key to understanding seed dormancy, *Plants (Basel)*, 2020, vol. 9, no. 4. <https://doi.org/10.3390/plants9040480>
- Chen, F., Nonogaki, H., Bradford, K. J., A gibberellin-regulated xyloglucan endotransglucosylase gene is expressed in the endosperm cap during tomato seed germination, *J. Exp. Bot.*, 2002, vol. 53, no. 367, pp. 215–223. <https://doi.org/10.1093/jexbot/53.367.215>
- Chen, F., Bradford, K.J., Expression of an expansin is associated with endosperm weakening during tomato seed germination, *Plant Physiol.*, 2000, vol. 124, pp. 1265–1274. <https://doi.org/10.1104/pp.124.3.1265>
- Chen, X., Börner, A., Xin, X., Nagel, M., He, J., Li, J., et al., Comparative proteomics at the critical node of vigor loss in wheat seeds differing in storability, *Front. Plant Sci.*, 2021, vol. 12, p. 707184. <https://doi.org/10.3389/fpls.2021.707184>
- Chen, H.H., Chu, P., Zhou, Y.L., Ding, Y., Li, Y., Liu, J., Jiang, L.W., Huang, S.Z., Ectopic expression of NnPER1, a *Nelumbo nucifera* 1-cysteine peroxidase, enhances seed longevity and stress tolerance in *Arabidopsis*, *Plant J.*, 2016, vol. 88, pp. 608–619. <https://doi.org/10.1111/tpj.13286>
- Cho, J., Ryu, J.-Y., Jeong, Y.-M., Park, J., Song, J.-J., Amasino, R.M., Noh, B., Noh, Y.-S., Control of seed germination by light-induced histone arginine demethylation activity, *Dev. Cell*, 2012, vol. 22, pp. 736–748. <https://doi.org/10.1016/j.devcel.2012.01.024>
- Clerkx, E.J., Blankestijn-De Vries, H., Ruys, G.J., Groot, S.P., Koornneef, M., Genetic differences in seed longevity of various *Arabidopsis* mutants, *Physiol. Plant*, 2004, vol. 121, pp. 448–461. <https://doi.org/10.1111/j.0031-9317.2004.00339.x>
- Dalling, J.W., Davis, A.S., Arnold, A.E., Sarmiento, C., Zalamea, P.-C., Extending plant defense theory to seeds, *Annu. Rev. Ecol. Evol. Syst.*, 2020, vol. 51, pp. 123–141. <https://doi.org/10.1146/annurev-ecolsys-012120-115156>
- de Souza Vidigal, D., Willems, L., van Arkel, J., Dekkers, B.J., Hilhorst, H.W., Bentsink, L., Galactinol as marker for seed longevity, *Plant Sci.*, 2016, vol. 246, pp. 112–118. <https://doi.org/10.1016/j.plantsci.2016.02.015>
- Dekkers, B.J.W., He, H., Hanson, J., Willems, L.A.J., Jamar, D.C.L., Cuff, G., Rajjou, L., Hilhorst, H.W.M., Bentsink, L., The *Arabidopsis* delay of germination 1 gene affects abscisic acid insensitive 5 (*ABI5*) expression and genetically interacts with *ABI3* during *Arabidopsis* seed development, *Plant J.*, 2016, vol. 85, no. 4, pp. 451–465. <https://doi.org/10.1111/tpj.13118>
- Deng, P., Bian, J., Yue, H., Feng, K., Wang, M., Du, X., Weining, S., Nie, X., Characterization of microRNAs and their targets in wild barley (*Hordeum vulgare* subsp. spontaneum) using deep sequencing, *Genome*, 2016, vol. 59, pp. 339–348. <https://doi.org/10.1139/gen-2015-0224>
- Dubois, M., Skirycz, A., Claeys, H., Maleux, K., Dhondt, S., De Bodt, S., et al., Ethylene response factor 6 acts as a central regulator of leaf growth under water-limiting conditions in *Arabidopsis*, *Plant Physiol.*, 2013, vol. 162, pp. 319–332. <https://doi.org/10.1104/pp.113.216341>
- Bicalho, E.M., Pinty-Marijuan, M., Morales, M., Müller, M., Munné-Bosch, S., Garcia, Q.S., Control of macaw palm seed germination by the gibberellin/abscisic acid balance, *Plant Biol.*, 2015, vol. 17, no. 5, pp. 990–996. <https://doi.org/10.1111/plb.12332>
- Eichmann, R., Richards, L., Schäfer, P., Hormones as go-betweens in plant microbiome assembly, *Plant J.*, 2021, vol. 105, no. 2, pp. 518–541. <https://doi.org/10.1111/tpj.15135>
- Fedak, H., Palusinska, M., Krzyczmonik, K., Brzezniak,

- L., Yatusovich, R., Pietras, Z., Kaczanowski, S., Swiezewski, S., Control of seed dormancy in Arabidopsis by a cis-acting noncoding antisense transcript, *Proc. Natl. Acad. Sci. USA*, 2016, vol. 113, pp. E7846–E7855. <https://doi.org/10.1073/pnas.1608827113>
- Fenollosa, E., Jené, L., Munné-Bosch, S., A rapid and sensitive method to assess seed longevity through accelerated aging in an invasive plant species, *Plant Methods*, 2020, vol. 16, p. 64. <https://doi.org/10.1186/s13007-020-00607-3>
- Fleming, M.B., Patterson, E.L., Reeves, P.A., Richards, C.M., Gaines, T.A., Walters, C., Exploring the fate of mRNA in aging seeds: Protection, destruction, or slow decay?, *J. Exp. Bot.*, 2018, vol. 69, pp. 4309–4321. <https://doi.org/10.1093/jxb/ery215>
- Fuerst, E.P., James, M.S., Pollard, A.T., Okubara, P.A., Defense enzyme responses in dormant wild oat and wheat caryopses challenged with a seed decay pathogen, *Front. Plant Sci.*, 2017, vol. 8, p. 2259. <https://doi.org/10.3389/fpls.2017.02259>
- Gagliardi, D., Cambiagno, D.A., Arce, A. L., Tomasi, A.H., Giacomelli, J.I., Ariel, F.D., Manavella, P.A., Dynamic regulation of chromatin topology and transcription by inverted repeat-derived small RNAs in sunflower, *Proc. Natl. Acad. Sci. USA*, 2019, vol. 116, pp. 17578–17583. <https://doi.org/10.1073/pnas.1903131116>
- Gerna, D., Arc, E., Holzknacht, M., Roach, T., Jansen-Dürr, P., Weiss, A.K., Kranner, I., *AtFAHD1a*: a new player influencing seed longevity and dormancy in Arabidopsis?, *Int. J. Mol. Sci.*, 2021, vol. 22, no. 6, p. 2997. <https://doi.org/10.3390/ijms22062997>
- Gianella, M., Balestrazzi, A., Ravasio, A., Mondoni, A., Börner, A., Guzzon, F., Comparative seed longevity under gene bank storage and artificial ageing: a case study in heteromorphic wheat wild relatives, *Plant Biol.*, 2022, vol. 24. <https://doi.org/10.1111/plb.13421>
- Gong, S., Ding, Y., Huang, S., Zhu, C., Identification of miRNAs and their target genes associated with sweet corn seed vigor by combined small RNA and degradome sequencing, *J. Agric. Food Chem.*, 2015, vol. 63, pp. 5485–5491. <https://doi.org/10.1021/acs.jafc.5b00522>
- Goyal, K., Walton, L.J., Tunnacliffe, A., LEA proteins prevent protein aggregation due to water stress, *Biochem. J.*, 2005, vol. 388, pp. 151–157. <https://doi.org/10.1042/BJ20041931>
- Groot, S.P.C., Bruinsma, J., Karssen, C.M., The role of endogenous gibberellins in seed and fruit development of tomato: studies with a gibberellin-deficient mutant, *Physiol. Plant.*, 1987, vol. 71, pp. 184–190. <https://doi.org/10.1111/j.1399-3054.1987.tb02865.x>
- Gu, D., Ji, R., He, C., Peng, T., Zhang, M., Duan, J., Xiong, C., Liu, X., Arabidopsis histone methyltransferase SUVH5 is a positive regulator of light-mediated seed germination, *Front. Plant Sci.*, 2019, vol. 10, 841. <https://doi.org/10.3389/fpls.2019.00841>
- Guo, G., Liu, X., Sun, F., Cao, J., Huo, N., et al., Wheat miR9678 affects seed germination by generating phased siRNAs and modulating abscisic acid/gibberellin signaling, *Plant Cell*, 2018, vol. 30, pp. 796–814. <https://doi.org/10.1105/tpc.17.00842>
- Hampton, J.G., TeKrony, D.M., Handbook of vigour test methods, 3rd ed., International Seed Testing Association, Zürich, Switzerland, 1995.
- Han, S.K., Sang, Y., Rodrigues, A., Biol, F., Wu, M.F., Rodriguez, P.L., Wagner, D., The SWI2/SNF2 chromatin remodeling ATPase BRAHMA represses abscisic acid responses in the absence of the stress stimulus in Arabidopsis, *Plant Cell*, 2012, vol. 24, pp. 4892–4906. <https://doi.org/10.1105/tpc.112.105114>
- Han, Q., Chen, K., Yan, D., Hao, G., Qi, J., Wang, C., Dirk, L.M.A., Bruce Downie, A., Gong, J., Wang, J., et al., ZmDREB2A regulates ZmGH3.2 and ZmRAFS, shifting metabolism towards seed aging tolerance over seedling growth, *Plant J.*, 2020, vol. 104, pp. 268–282. <https://doi.org/10.1111/tpj.14922>
- Hasanuzzaman, M., Parvin, K., Bardhan, K., Nahar, K., Anee, T.I., Masud, A.A.C., Fotopoulos, V., Biostimulants for the regulation of reactive oxygen species metabolism in plants under abiotic stress, *Cells*, 2021, vol. 10, 2537. <https://doi.org/10.3390/cells10102537>
- Helt, C.E., Cliby, W.A., Keng, P.C., Bambara, R.A., O'Reilly, M.A., Ataxia telangiectasia mutated (ATM) and ATM and Rad3-related protein exhibit selective target specificities in response to different forms of DNA damage, *J. Biol. Chem.*, 2005, vol. 280, no. 2, pp. 1186–1192. <https://doi.org/10.1074/jbc.M410873200>
- Hendry, G., Oxygen free radical process and seed longevity, *Seed Sci. Res.*, 1993, vol. 3, pp. 141–153. <https://doi.org/10.1017/S0960258500001720>
- Hilhorst, H.W.M., A critical update on seed dormancy. I. Primary dormancy, *Seed Sci. Res.*, 1995, vol. 5, pp. 61–73. <https://doi.org/10.1017/S0960258500002634>
- Hilhorst, H.W.M., Karssen, C.M., Seed dormancy and germination: the role of abscisic acid and gibberellins and the importance of hormone mutants, *Plant Growth Regul.*, 1992, vol. 11, pp. 225–238. <https://doi.org/10.1007/BF00024561>
- Hu, J., Zhang, Y., Wang, J., Zhou, Y., Glycerol affects root development through regulation of multiple pathways in Arabidopsis, *PLoS One*, 2014, vol. 9, no. 1, e86269. <https://doi.org/10.1371/journal.pone.0086269>
- Hu, Y., Han, X., Yang, M., Zhang, M., Pan, J., Yu,

- D., The transcription factor inducer of CBF expression 1 interacts with abscisic acid insensitive 5 and DELLA proteins to fine-tune abscisic acid signaling during seed germination in *Arabidopsis*, *Plant Cell*, 2019, vol. 31, no. 7, pp. 1520–1538. <https://doi.org/10.1105/tpc.18.00825>
- Hu, Y., Yu, D., Brassinosteroid insensitive 2 interacts with abscisic acid insensitive 5 to mediate the antagonism of brassinosteroids to abscisic acid during seed germination in *Arabidopsis*, *Plant Cell*, 2014, vol. 26, no. 11, pp. 4394–4408. <https://doi.org/10.1105/tpc.114.130849>
- Huang, Z., Boubriak, I., Osborne, D.J., Dong, M., Guterma, Y., Possible role of pectin-containing mucilage and dew in repairing embryo DNA of seeds adapted to desert conditions, *Ann. Bot.*, 2008, vol. 101, pp. 277–283. <https://doi.org/10.1093/aob/mcm089>
- Huang, J., Cai, M., Long, Q., Liu, L., Lin, Q., Jiang, L., Chen, S., Wan, J., OsLOX2, a rice type I lipoxygenase, confers opposite effects on seed germination and longevity, *Transgenic Res.*, 2014, vol. 23, pp. 643–655. <https://doi.org/10.1007/s11248-014-9803-2>
- Hundertmark, M., Buitink, J., Leprince, O., Hincha, D.K., The reduction of seed-specific dehydrins reduces seed longevity in *Arabidopsis thaliana*, *Seed Sci. Res.*, 2011, vol. 21, pp. 165–173. <https://doi.org/10.1017/S0960258511000079>
- Carter, J.L., Garrard, L.A., West, S.H., Effect of gibberellic acid on starch-degrading enzymes in leaves of *Digitaria decumbens*, *Phytochemistry*, 1973, vol. 12, pp. 251–254. [https://doi.org/10.1016/0031-9422\(73\)80002-0](https://doi.org/10.1016/0031-9422(73)80002-0)
- Jacobsen, S.E., Binkowski, K.A., Olszewski, N.E., SPINDLY, a tetratricopeptide repeat protein involved in gibberellin signal transduction in *Arabidopsis*, *Proc. Natl. Acad. Sci. USA*, 1996, vol. 93, pp. 9292–9296. <https://doi.org/10.1073/pnas.93.17.9292>
- Jacobsen, S.E., Olszewski, N.E., Mutations at the SPINDLY locus of *Arabidopsis* alter gibberellin signal transduction, *Plant Cell*, 1993, vol. 5, pp. 887–896. <https://doi.org/10.1105/tpc.5.8.887>
- Johnston-Monje, D., Gutiérrez, J.P., Lopez-Lavalle, L.A.B., Seed-transmitted bacteria and fungi dominate juvenile plant microbiomes, *Front. Microbiol.*, 2021, vol. 12, 737616. <https://doi.org/10.3389/fmicb.2021.737616>
- Joosen, R.V.L., Kodde, J., Willems, L.A.J., Ligterink, W., van der Plas, L.H.W., Hilhorst, H.W.M., GERMINATOR: a software package for high-throughput scoring and curve fitting of *Arabidopsis* seed germination, *Plant J.*, 2010, vol. 62, pp. 148–159. <https://doi.org/10.1111/j.1365-3113X.2009.04116.x>
- Zinsmeister, J., Lalanne, D., Terrasson, E., et al., ABI5 is a regulator of seed maturation and longevity in legumes, *Plant Cell*, 2016, vol. 28, no. 11, pp. 2735–2754. <https://doi.org/10.1105/tpc.16.00470>
- Kamiya, Y., Garcia-Martinez, J.L., Regulation of gibberellin biosynthesis by light, *Curr. Opin. Plant Biol.*, 1999, vol. 2, pp. 398–403. [https://doi.org/10.1016/s1369-5266\(99\)00012-6](https://doi.org/10.1016/s1369-5266(99)00012-6)
- Karssen, C.M., Zagorsky, S., Kepczynski, J., Groot, S.P.C., Key role for endogenous gibberellins in the control of seed germination, *Ann. Bot.*, 1989, vol. 63, pp. 71–80. <https://doi.org/10.1093/oxfordjournals.aob.a087730>
- Kawakatsu, T., Nery, J.R., Castanon, R., Ecker, J.R., Dynamic DNA methylation reconfiguration during seed development and germination, *Genome Biol.*, 2017, vol. 18, 171. <https://doi.org/10.1186/s13059-017-1251-x>
- Kim, J.Y., Kwak, K.J., Jung, H.J., Lee, H.J., Kang, H., MicroRNA402 affects seed germination of *Arabidopsis thaliana* under stress conditions via targeting DEMETER-LIKE Protein3 mRNA, *Plant Cell Physiol.*, 2010, vol. 51, pp. 1079–1083. <https://doi.org/10.1093/pcp/pcq072>
- Kimura, M., Nambara, E., Stored and neosynthesized mRNA in *Arabidopsis* seeds: effects of cycloheximide and controlled deterioration treatment on the resumption of transcription during imbibition, *Plant Mol. Biol.*, 2010, vol. 73, pp. 119–129. <https://doi.org/10.1007/s11103-010-9603-x>
- Knox-Brown, P., Rindfleisch, T., G nther, A., Balow, K., Bremer, A., Walther, D., Miettinen, M.S., Hincha, D.K., Thallhammer, A., Similar yet different – structural and functional diversity among *Arabidopsis thaliana* LEA 4 proteins, *Int. J. Mol. Sci.*, 2020, vol. 21, 2794. <https://doi.org/10.3390/ijms21082794>
- Koornneef, M., Bentsink, L., Hilhorst, H., Seed dormancy and germination, *Curr. Opin. Plant Biol.*, 2002, vol. 5, pp. 33–36. [https://doi.org/10.1016/s1369-5266\(01\)00219-9](https://doi.org/10.1016/s1369-5266(01)00219-9)
- Koornneef, M., Karssen, C.M., Seed dormancy and germination, in: *Arabidopsis*, Meyerowitz, E.M., Somerville, C.R., Eds., Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press, 1994, pp. 313–334.
- Kucera, B., Cohn, M.A., Leubner-Metzger, G., Plant hormone interactions during seed dormancy release and germination, *Seed Sci. Res.*, 2005, vol. 15, pp. 281–307. <https://doi.org/10.1079/SSR2005218>
- Kumar, A., Verma, J.P., Does plant-microbe interaction confer stress tolerance in plants: A review, *Microbiol. Res.*, 2018, vol. 207, pp. 41–52. <https://doi.org/10.1016/j.micres.2017.11.004>
- Kurek, K., Plitta-Michalak, B., Ratajczak, E., Reactive oxygen species as potential drivers of the seed aging

- process, *Plants (Basel)*, 2019, vol. 8, 174. <https://doi.org/10.3390/plants8060174>
- Lee, J.-S., Velasco-Punzalan, M., Pacleb, M., Valdez, R., Kretschmar, T., McNally, K.L., Ismail, A.M., Cruz, P.C.S., Sackville Hamilton, N.R., Hay, F.R., Variation in seed longevity among diverse Indica rice varieties, *Ann. Bot.*, 2019, vol. 124, pp. 447–460. <https://doi.org/10.1093/aob/mcz093>
- Lee, S., Cheng, H., King, K.E., Wang, W., He, Y., Hus-sain, A., Lo, J., Harberd, N.P., Peng, J., Gibberellin regulates Arabidopsis seed germination via RGL2, a GAI/RGA-like gene whose expression is up-regulated following imbibition, *Genes Dev.*, 2002, vol. 16, pp. 646–658. <https://doi.org/10.1101/gad.969002>
- Lee, J.-S., Kwak, J., Cho, J.-H., Chebotarov, D., Yoon, M.-R., Lee, J.-S., Hamilton, N.R.S., Hay, F.R., A high proportion of beta-tocopherol in vitamin E is associated with poor seed longevity in rice produced under temperate conditions, *Plant Genet. Resour.*, 2019, vol. 17, pp. 375–378. <https://doi.org/10.1017/S147926211900008X>
- Lee, J.-S., Kwak, J., Yoon, M.-R., Lee, J.-S., Hay, F.R., Contrasting tocol ratios associated with seed longevity in rice variety groups, *Seed Sci. Res.*, 2017, vol. 27, pp. 273–280. <https://doi.org/10.1017/S0960258517000265>
- Leubner-Metzger, G., Seed after-ripening and over-expression of class I beta-1,3-glucanase confer maternal effects on tobacco tests rupture and dormancy release, *Planta*, 2002, vol. 215, pp. 959–968. <https://doi.org/10.1007/s00425-002-0837-y>
- Leubner-Metzger, G., Functions and regulation of β -1,3-glucanase during seed germination, dormancy release and after-ripening, *Seed Sci. Res.*, 2003, vol. 13, pp. 17–34. <https://doi.org/10.1079/SSR2002121>
- Li, G., Na, Y.-W., Kwon, S.-W., Park, Y.-J., Association analysis of seed longevity in rice under conventional and high-temperature germination conditions, *Plant Syst. Evol.*, 2014, vol. 300, pp. 389–402. <https://doi.org/10.1007/s00606-013-0889-4>
- Li, X., Liu, Q., Liu, J., Long non-coding RNAs: Discoveries, mechanisms, and research strategies in seeds, *Genes (Basel)*, 2023, vol. 14, 2214. <https://doi.org/10.3390/genes14122214>
- Liang, W., Dong, H., Guo, X., Rodríguez, V., Cheng, M., Identification of long-lived and stable mRNAs in the aged seeds of wheat, *Seed Biol.*, 2023, vol. 2, no. 14. <https://doi.org/10.48130/SeedBio-2023-0014>
- Liu, P.P., Montgomery, T.A., Fahlgren, N., Kasschau, K.D., Nonogaki, H., Repression of auxin response factor 10 by microRNA160 is critical for seed germination and post-germination stages, *Plant J.*, 2007, vol. 52, pp. 133–146. <https://doi.org/10.1111/j.1365-313X.2007.03218.x>
- Liu, W., Pan, X., Li, Y., Duan, Y., Min, J., Liu, S., Sheng, X., Li, X., Detection and validation of QTLs associated with seed longevity in rice (*Oryza sativa* L.), *Plant Breed.*, 2018, vol. 137, pp. 546–552. <https://doi.org/10.1111/pbr.12611>
- Long, Q., Zhang, W., Wang, P., Shen, W., Zhou, T., Liu, N., Wang, R., Jiang, L., Huang, J., Wang, Y., Molecular genetic characterization of rice seed lipoxygenase 3 and assessment of its effects on seed longevity, *J. Plant Biol.*, 2013, vol. 56, pp. 232–242. <https://doi.org/10.1007/s12374-013-0085-7>
- Luján-Soto, E., Dinkova, T.D., Time to wake up: Epi-genetic and small-RNA-mediated regulation during seed germination, *Plants (Basel)*, 2021, vol. 10, 236. <https://doi.org/10.3390/plants10020236>
- Magome, H., Yamaguchi, S., Hanada, A., Kamiya, Y., Oda, K., The DDF1 transcriptional activator upregulates expression of a gibberellin-deactivating gene, GA2ox7, under high-salinity stress in *Arabidopsis*, *Plant J. Cell Mol. Biol.*, 2008, vol. 56, pp. 613–626. <https://doi.org/10.1111/j.1365-313X.2008.03627.x>
- Mao, Z., Sun, W., Arabidopsis seed-specific vacuolar aquaporins are involved in maintaining seed longevity under the control of abscisic acid insensitive 3, *J. Exp. Bot.*, 2015, vol. 66, pp. 4781–4794. <https://doi.org/10.1093/jxb/erv244>
- Miao, C., Wang, Z., Zhang, L., et al., The grain yield modulator *miR156* regulates seed dormancy through the gibberellin pathway in rice, *Nat. Commun.*, 2019, vol. 10, 3822. <https://doi.org/10.1038/s41467-019-11830-5>
- Millar, A.A., Lohe, A., Wong, G., Biology and function of *miR159* in plants, *Plants (Basel)*, 2019, vol. 8, 255. <https://doi.org/10.3390/plants8080255>
- Molitor, A.M., Bu, Z., Yu, Y., Shen, W., Arabidopsis AL PHD-PRC1 complexes promote seed germination through H3K4me3-to-H3K27me3 chromatin state switch in repression of seed developmental genes, *PLoS Genet.*, 2014, vol. 10, e1004091. <https://doi.org/10.1371/journal.pgen.1004091>
- Møller, I.M., Plant mitochondria and oxidative stress: Electron transport, NADPH turnover, and metabolism of reactive oxygen species, *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 2001, vol. 52, pp. 561–591. <https://doi.org/10.1146/annurev.arplant.52.1.561>
- Sano, N., Takebayashi, Y., To, A., Mhiri, C., Rajjou, L.C., Nakagami, H., Kanekatsu, M., Shotgun proteomic analysis highlights the roles of long-lived mRNAs and de novo transcribed mRNAs in rice seeds upon imbibition, *Plant Cell Physiol.*, 2019, vol. 60, pp. 2584–2596. <https://doi.org/10.1093/pcp/pcz164>
- Nagel, M., Alqudah, A.M., Bailly, M., Rajjou, L., Pist-rick, S., Matzig, G., Börner, A., Kranner, I., Novel

- loci and a role for nitric oxide for seed dormancy and preharvest sprouting in barley, *Plant Cell Environ.*, 2019, vol. 42, pp. 1318–1327. <https://doi.org/10.1111/pce.13483>
- Nagel, M., Börner, A., The longevity of crop seeds stored under ambient conditions, *Seed Sci. Res.*, 2010, vol. 20, pp. 1–12. <https://doi.org/10.1017/S0960258509990213>
- Nagel, M., Kranner, I., Neumann, K., Rolletschek, H., Seal, C.E., Colville, L., Fernández-Marrón, B., Börner, A., Genome-wide association mapping and biochemical markers reveal that seed aging and longevity are intricately affected by genetic background and developmental and environmental conditions in barley, *Plant Cell Environ.*, 2015, vol. 38, pp. 1011–1022. <https://doi.org/10.1111/pce.12474>
- Nagel, M., Rosenhauer, M., Willner, E., Snowdon, R.J., Friedt, W., Börner, A., Seed longevity in oilseed rape (*Brassica napus* L.) – genetic variation and QTL mapping, *Plant Genet. Resour.*, 2011, vol. 9, pp. 260–263. <https://doi.org/10.1017/S1479262111000372>
- Nakajima, S., Ito, H., Tanaka, R., Tanaka, A., Chlorophyll *b* reductase plays an essential role in maturation and storability of *Arabidopsis* seeds, *Plant Physiol.*, 2012, vol. 160, pp. 261–273. <https://doi.org/10.1104/pp.112.196881>
- Narsai, R., Gouil, Q., Secco, D., Srivastava, A., Karpievitch, Y.V., Liew, L.C., Lister, R., Lewsey, M.G., Whelan, J., Extensive transcriptomic and epigenomic remodeling occurs during *Arabidopsis thaliana* germination, *Genome Biol.*, 2017, vol. 18, 172. <https://doi.org/10.1186/s13059-017-1251-x>
- Nguyen, T.-P., Keizer, P., van Eeuwijk, F., Smeekens, S., Bentsink, L., Natural variation for seed longevity and seed dormancy are negatively correlated in *Arabidopsis*, *Plant Physiol.*, 2012, vol. 160, pp. 2083–2092. <https://doi.org/10.1104/pp.112.206649>
- Nicoles, R., Ruiz-Pastor, C.M., Arjona-Mudarra, P., Casac, J., Renard, J., Bueso, E., Mateos, R., Serano, R., Gadea, J., Transcription factor *DOF4.1* regulates seed longevity in *Arabidopsis* via seed permeability and modulation of seed storage protein accumulation, *Front. Plant Sci.*, 2022, vol. 13, 915184. <https://doi.org/10.3389/fpls.2022.915184>
- Nisarga, K.N., Vemanna, R.S., Chandrashekar, B.K., Rao, H., Vennapusa, A.R., Narasimaha, A., Markarla, U., Basavaiah, M.R., Aldo-ketoreductase 1 (AKR1) improves seed longevity in tobacco and rice by detoxifying reactive cytotoxic compounds generated during aging, *Rice*, 2017, vol. 10, 11. <https://doi.org/10.1186/s12284-017-0148-3>
- Nonogaki, H., Gee, O.H., Bradford, K.J., A germination-specific endo- β -mannanase gene is expressed in the micropylar endosperm cap of tomato seeds, *Plant Physiol.*, 2000, vol. 123, pp. 1235–1245. <https://doi.org/10.1104/pp.123.4.1235>
- Nonogaki, H., The long-standing paradox of seed dormancy unfolded?, *Trends Plant Sci.*, 2019, vol. 24, pp. 989–998. <https://doi.org/10.1016/j.tplants.2019.06.011>
- Ogawa, M., Hanada, A., Yamauchi, Y., Kuwahara, A., Kamiya, Y., Yamaguchi, S., Gibberellin biosynthesis and response during *Arabidopsis* seed germination, *Plant Cell*, 2003, vol. 15, pp. 1591–1604. <https://doi.org/10.1105/tpc.011650>
- Ogé, L., Bourdais, G., Bove, J., Collet, B., Godin, B., Granier, F., Boutin, J.-P., Job, D., Jullien, M., Grappin, P., Protein repair L-isoaspartyl methyltransferase1 is involved in both seed longevity and germination vigor in *Arabidopsis*, *Plant Cell*, 2008, vol. 20, pp. 3022–3037. <https://doi.org/10.1105/tpc.108.058479>
- Olszewski, N., Tai-Ping, S., Gubler, F., Gibberellin signaling: biosynthesis, catabolism, and response pathways, *Plant Cell*, 2002, vol. 14, pp. S61–S80. <https://doi.org/10.1105/tpc.010476>
- Park, J., Oh, D.-H., Dassanayake, M., Nguyen, K.T., Ogas, J., Choi, G., Sun, T.-P., Gibberellin signaling requires chromatin remodeler PICKLE to promote vegetative growth and phase transitions, *Plant Physiol.*, 2017, vol. 173, pp. 1463–1474. <https://doi.org/10.1104/pp.16.01471>
- Pirredda, M., Facanás-Pueyo, I., Ocate-Sánchez, L., Mira, S., Seed longevity and ageing: A review on physiological and genetic factors with an emphasis on hormonal regulation, *Plants*, 2024, vol. 13, 41. <https://doi.org/10.3390/plants13010041>
- Qi, J., Song, C.P., Wang, B., Zhou, J., Kangasjärvi, J., Zhu, J.K., et al., Reactive oxygen species signaling and stomatal movement in plant responses to drought stress and pathogen attack, *J. Integr. Plant Biol.*, 2018, vol. 60, pp. 805–826. <https://doi.org/10.1111/jipb.12654>
- Ramtekey, V., Cherukuri, S., Kumar, S., et al., Seed longevity in legumes: deeper insights into mechanisms and molecular perspectives, *Front. Plant Sci.*, 2022, vol. 13, 918206. <https://doi.org/10.3389/fpls.2022.918206>
- Ratajczak, W., Rył, A., Mizerski, A., Walczakiewicz, K., Sipak, O., Laszczyńska, M., Immunomodulatory potential of gut microbiome-derived short-chain fatty acids (SCFAs), *Acta Biochim. Pol.*, 2019, vol. 66, pp. 1–12. https://doi.org/10.18388/abp.2018_2648
- Renard, J., Martínez-Almonacid, I., Queralta Castillo, I., et al., Apoplastic lipid barriers regulated by conserved homeobox transcription factors extend seed longevity in multiple plant species, *New Phytol.*, 2021, vol. 231, pp. 679–694. <https://doi.org/10.1111/nph.17399>
- Renard, J., Nicoles, R., Martínez-Almonacid, I., et al.,

- Identification of novel seed longevity genes related to oxidative stress and seed coat by genome-wide association studies and reverse genetics, *Plant Cell Environ.*, 2020, vol. 43, pp. 2523–2539. <https://doi.org/10.1111/pce.13822>
- Reyes, J.L., Chua, N.H., ABA induction of *miR159* controls transcript levels of two *MYB* factors during *Arabidopsis* seed germination, *Plant J.*, 2007, vol. 49, pp. 592–606. <https://doi.org/10.1111/j.1365-3113X.2006.02980.x>
- Richards, D.E., King, K.E., Aitali, T., Harberd, N.P., How gibberellin regulates plant growth and development: A molecular genetic analysis of gibberellin signaling, *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 2001, vol. 52, pp. 67–88. <https://doi.org/10.1146/annurev.arplant.52.1.67>
- Righetti, K., Vu, J.L., Pelletier, S., et al., Inference of longevity-related genes from a robust coexpression network of seed maturation identifies regulators linking seed storability to biotic defense-related pathways, *Plant Cell*, 2015, vol. 27, pp. 2692–2708. <https://doi.org/10.1105/tpc.15.00632>
- Roach, T., Nagel, M., Börner, A., Eberle, C., Kraner, I., Changes in tocochromanols and glutathione reveal differences in the mechanisms of seed ageing under seedbank conditions and controlled deterioration in barley, *Environ. Exp. Bot.*, 2018, vol. 156, pp. 8–15. <https://doi.org/10.1016/j.envexpbot.2018.08.027>
- Rodríguez, M.V., Barrero, J.M., Corbineau, F., Gubler, F., Benech-Arnold, R.L., Dormancy in cereals (not too much, not so little): about the mechanisms behind this trait, *Seed Sci. Res.*, 2015, vol. 25, pp. 99–119. <https://doi.org/10.1017/S0960258515000021>
- Roulé, T., Christ, A., Hussain, N., et al., The lncRNA MARS modulates the epigenetic reprogramming of the marneral cluster in response to ABA, *Mol. Plant.*, 2022, vol. 15, pp. 840–856. <https://doi.org/10.1016/j.molp.2022.02.007>
- Saighani, K., Kondo, D., Sano, N., et al., Correlation between seed longevity and RNA integrity in the embryos of rice seeds, *Plant Biotechnol. (Tokyo)*, 2021, vol. 38, pp. 277–283. <https://doi.org/10.5511/plantbiotechnology.21.0422a>
- Sajeev, N., Bai, B., Bentsink, L., Seeds: a unique system to study translational regulation, *Trends Plant Sci.*, 2019, vol. 24, pp. 487–495. <https://doi.org/10.1016/j.tplants.2019.03.011>
- Sano, N., Rajjou, L., North, H.M., Debeaujon, I., Marion-Poll, A., Seo, M., Staying alive: molecular aspects of seed longevity, *Plant Cell Physiol.*, 2016, vol. 57, pp. 660–674. <https://doi.org/10.1093/pcp/pcv186>
- Sano, N., Rajjou, L., North, H.M., Lost in translation: physiological roles of stored mRNAs in seed germination, *Plants (Basel)*, 2020, vol. 9, 347. <https://doi.org/10.3390/plants9030347>
- Sano, N., Permana, H., Kumada, R., et al., Proteomic analysis of embryonic proteins synthesized from long-lived mRNAs during germination of rice seeds, *Plant Cell Physiol.*, 2012, vol. 53, pp. 687–698. <https://doi.org/10.1093/pcp/pcs024>
- Sarmiento, C., Zalamea, P.-C., Dalling, J.W., Davis, A.S., Stump, S.M. et al., Soilborne fungi have host affinity and host-specific effects on seed germination and survival in a lowland tropical forest, *PNAS*, 2017, vol. 114, pp. 11458–11463. <https://doi.org/10.1073/pnas.1703237114>
- Sattler, S.E., Gilliland, L.U., Magallanes-Lundback, M., Pollard, M., DellaPenna, D., Vitamin E is essential for seed longevity and for preventing lipid peroxidation during germination, *Plant Cell*, 2004, vol. 16, pp. 1419–1432. <https://doi.org/10.1105/tpc.021360>
- Shen, W., Yao, X., Ye, T., Ma, S., Liu, X., Yin, X., Wu, Y., *Arabidopsis* aspartic protease *ASPG1* affects seed dormancy, seed longevity and seed germination, *Plant Cell Physiol.*, 2018, vol. 59, pp. 1415–1431. <https://doi.org/10.1093/pcp/pcy070>
- Shin, J.-H., Kim, S.-R., An, G., Rice aldehyde dehydrogenase7 is needed for seed maturation and viability, *Plant Physiol.*, 2009, vol. 149, pp. 905–915. <https://doi.org/10.1104/pp.108.130716>
- Shu, K., Liu, X.D., Xie, Q., He, Z.H., Two faces of one seed: hormonal regulation of dormancy and germination, *Mol. Plant*, 2016, vol. 9, pp. 34–45. <https://doi.org/10.1016/j.molp.2015.08.010>
- Siles, L., Alegre, L., González-Solis, A., Cahoon, E.B., Munné-Bosch, S., Transcriptional regulation of vitamin E biosynthesis during germination of dwarf fan palm seeds, *Plant Cell Physiol.*, 2018, vol. 59, pp. 2490–2501. <https://doi.org/10.1093/pcp/pcy170>
- Silverstone, A.L., Jung, H.S., Dill, A., Kawaide, H., Kamiya, Y., Sun, T.P., Repressing a repressor: gibberellin-induced rapid reduction of the RGA protein in *Arabidopsis*, *Plant Cell*, 2001, vol. 13(7), pp. 1555–1566. <https://doi.org/10.1105/tpc.010047>
- Solberg, S.II., Yndgaard, F., Andreasen, C., von Bothmer, R., Loskutov, I.G., Asdal, E., Long-Term Storage and Longevity of Orthodox Seeds: A Systematic Review, *Front. Plant Sci.*, 2020, vol. 11, pp. 1007. <https://doi.org/10.3389/fpls.2020.01007>
- Song, Y., Lv, Z., Wang, Y., Li, C., Jia, Y., Zhu, Y., Cao, M., Zhou, Y., Zeng, X., Wang, Z., Zhang, L., Di, H., Identification of miRNAs Mediating Seed Storability of Maize during Germination Stage by High-Throughput Sequencing, Transcriptome and Degradome Sequencing, *Int J Mol Sci.*, 2022, vol. 23(20), pp. 12339. <https://doi.org/10.3390/ijms232012339>

- Steber, C.M., Cooney, S.E., McCourt, P., *Isolation of the GA-response mutant sly1 as a suppressor of ABI1-1 in Arabidopsis thaliana*, *Genetics*, 1998, vol. 149, pp. 509–521. <https://doi.org/10.1093/genetics/149.2.509>
- Steber, C.M., McCourt, P., *A role for brassinosteroids in germination in Arabidopsis*, *Plant Physiol.*, 2001, vol. 125(2), pp. 763–769. <https://doi.org/10.1104/pp.125.2.763>
- Sugliani, M., Rajjou, L., Clercx, E.J.M., Koornneef, M., Soppe, W.J.J., *Natural modifiers of seed longevity in the Arabidopsis mutants Absciscic Acid Insensitive3-5 (Abi3-5) and Leafy Cotyledon1-3 (Lec1-3)*, *New Phytologist*, 2009, vol. 184(4), pp. 898–908. <https://doi.org/10.1111/j.1469-8137.2009.03000.x>
- Sun, W.Q., Leopold, A.C., *Glassy state and seed storage stability: a viability equation analysis*, *Ann. Bot.*, 1994, vol. 74, pp. 601–604. <https://doi.org/10.1006/anbo.1994.1160>
- Tanaka, M., Kikuchi, A., Kamada, H., *The Arabidopsis histone deacetylases hda6 and hda19 contribute to the repression of embryonic properties after germination*, *Plant Physiol.*, 2007, vol. 146, pp. 149–161. <https://doi.org/10.1104/pp.107.111674>
- Taylor, R.E., Waterworth, W., West, C.E., Foyer, C.H., *WHIRLY proteins maintain seed longevity by effects on seed oxygen signalling during imbibition*, *Biochem. J.*, 2023, vol. 480(13), pp. 941–956. <https://doi.org/10.1042/BCJ20230008>
- Toyomasu, T., Kawaide, H., Mitsunashi, W., Inoue, Y., Kamiya, Y., *Phytochrome regulates gibberellin biosynthesis during germination of photoblastic lettuce seeds*, *Plant Physiol.*, 1998, vol. 118, pp. 1517–1523. <https://doi.org/10.1104/pp.118.4.1517>
- Tunnacliffe, A., Hinch, D., Leprince, O., Macherel, D., *LEA Proteins: versatility of form and function*, In *Dormancy and Resistance in Harsh Environments* (L. Esther, C. Joan, C. Melody), Berlin: Springer. 2010. pp. 91–108. https://doi.org/10.1007/978-3-642-12422-8_6
- Walker, J., Gao, H., Zhang, J. et al., *Sexual-lineage-specific DNA methylation regulates meiosis in Arabidopsis*, *Nat Genet.*, 2018, vol. 50, pp. 130–137. <https://doi.org/10.1038/s41588-017-0008-5>
- Wang, B., Wang, S., Tang, Y., Jiang, L., He, W., Lin, Q., Yu, F., Wang, L., *Transcriptome-wide characterization of seed aging in rice: identification of specific long-lived mRNAs for seed longevity*, *Front. Plant Sci.*, 2022, vol. 13, pp. 857390. <https://doi.org/10.3389/fpls.2022.857390>
- Wang, L., Liu, H., Li, D., Chen, H., *Identification and characterization of maize microRNAs involved in the very early stage of seed germination*, *BMC Genom.*, 2011, vol. 12, pp. 1–10. <https://doi.org/10.1186/1471-2164-12-154>
- Wang, Y., Cui, Y., Hu, G., et al., *Reduced bioactive gibberellin content in rice seeds under low temperature leads to decreased sugar consumption and low seed germination rates*, *Plant Physiol. Biochem.*, 2018, vol. 133, pp. 1–10. <https://doi.org/10.1016/j.plaphy.2018.10.020>
- Wang, Y., Li, L., Ye, T., Zhao, S., Liu, Z., Feng, Y.Q., Wu, Y., *Cytokinin antagonizes ABA suppression to seed germination of Arabidopsis by downregulating ABI5 expression*, *Plant J.*, 2011, vol. 68(2), pp. 249–261. <https://doi.org/10.1111/j.1365-313X.2011.04683.x>
- Waszczak, C., Carmody, M., Kangasjärvi, J., *Reactive oxygen species in plant signaling*, *Annu Rev Plant Biol.*, 2018, vol. 69, pp. 209–236. <https://doi.org/10.1146/annurev-arplant-042817-040322>
- Waterworth, W.M., Latham, R., Wang, D., Alsharif, M., West, C.E., *Seed DNA damage responses promote germination and growth in Arabidopsis thaliana*, *Proc. Natl. Acad. Sci. USA*, 2022, vol. 119, pp. 1–8. <https://doi.org/10.1073/pnas.2202172119>
- Waterworth, W.M., Footitt, S., Bray, C.M., Finch-Savage, W.E., West, C.E., *DNA damage checkpoint kinase ATM regulates germination and maintains genome stability in seeds*, *Proc. Natl. Acad. Sci. USA*, 2016, vol. 113, pp. 9647–9652. <https://doi.org/10.1073/pnas.1608829113>
- Waterworth, W.M., Masnavi, G., Bhardwaj, R.M., Jiang, Q., Bray, C.M., West, C.E., *A plant DNA ligase is an important determinant of seed longevity*, *Plant J.*, 2010, vol. 63(6), pp. 848–860. <https://doi.org/10.1111/j.1365-313X.2010.04285.x>
- Wei, Y., Xu, H., Diao, L., Zhu, Y., Xie, H., Cai, Q., Wu, F., Wang, Z., Zhang, J., Xie, H., *Protein repair L-isoaspartyl methyltransferase 1 (PIMT1) in rice improves seed longevity by preserving embryo vigor and viability*, *Plant Mol. Biol.*, 2015, vol. 89, pp. 475–492. <https://doi.org/10.1007/s11103-015-0383-1>
- Wen, C.-K., Chang, C., *Arabidopsis RGL1 encodes a negative regulator of gibberellin responses*, *Plant Cell*, 2002, vol. 14, pp. 87–100. <https://doi.org/10.1105/tpc.010325>
- Wiebach, J., Nagel, M., Burner, A., Altmann, T., Riewe, D., *Age-dependent loss of seed viability is associated with increased lipid oxidation and hydrolysis*, *Plant Cell Environ.*, 2019, vol. 43, no. 2, pp. 303–314. <https://doi.org/10.1111/pce.13651>
- Wozny, D., Kramer, K., Finkemeier, I., Acosta, I.F., Koornneef, M., *Genes for seed longevity in barley identified by genomic analysis on near isogenic lines*, *Plant Cell Environ.*, 2018, vol. 41(9), pp. 1895–1911. <https://doi.org/10.1111/pce.13330>
- Wu, C.T., Leubner-Metzger, G., Meins Jr, F., Bradford, K.J., *Class I β -1,3-glucanase and chitinase are expressed specifically in the micropylar endosperm of*

- tomato seeds prior to radicle emergence, *Plant Physiol.*, 2001, vol. 126, pp. 1299–1313. <https://doi.org/10.1104/pp.126.3.1299>
- Wu, F., Luo, X., Wang, L., Wei, Y., Li, J., Xie, H., Zhang, J., and Xie, G., *Genome-wide association study reveals the QTLs for seed storability in world rice core collections*, *Plants*, 2021, vol. 10, pp. 812. <https://doi.org/10.3390/plants10040812>
- Wu, J., Liu, C., Liu, Z., Li, S., Li, D., Liu, S., Huang, X., Liu, S., and Yukawa, Y., *Pol III-Dependent CabageBoNR8Long ncRNA Affects Seed Germination and Growth in Arabidopsis*, *Plant Cell Physiol.*, 2019, vol. 60, pp. 421–435. <https://doi.org/10.1093/pcp/pcy220>
- Xu, H., Wei, Y., Zhu, Y., Lian, L., Xie, H., Cai, Q., Chen, Q., Lin, Z., Wang, Z., and Xie, H., *Anti-sense suppression of LOX3 gene expression in rice endosperm enhances seed longevity*, *Plant Biotechnol. J.*, 2015, vol. 13, pp. 526–539. <https://doi.org/10.1111/pbi.12277>
- Yamaguchi, S., Kamiya, Y., Sun, T.P., *Distinct cell-specific expression patterns of early and late gibberellin biosynthetic genes during Arabidopsis seed germination*, *Plant J.*, 2001, vol. 28, pp. 443–453. <https://doi.org/10.1046/j.1365-3113x.2001.01168.x>
- Yang, C., Li, X., Chen, S., Liu, C., Yang, L., Li, K., Liao, J., Zheng, X., Li, H., Li, Y., Zeng, S., Zhuang, X., Rodriguez, P.L., Luo, M., Wang, Y., and Gao, C., *ABI5-FLZ13 module transcriptionally represses growth-related genes to delay seed germination in response to ABA*, *Plant Commun.*, 2023, vol. 4(6), pp. 100636. <https://doi.org/10.1016/j.xplc.2023.100636>
- Yazdanpanah, F., Maurino, V.G., Mettler-Altmann, T., Buijs, G., Bailly, M., Karimi Jashni, M., Willems, L., Sergeeva, L.I., Rajjou, L., and Hilhorst, H.W., *NADP-MALIC enzyme 1 affects germination after seed storage in Arabidopsis thaliana*, *Plant Cell Physiol.*, 2019, vol. 60, pp. 318–328. <https://doi.org/10.1093/pcp/pcy213>
- Zhang, X., Dong, J., Deng, F., et al., *The long non-coding RNA lncRNA973 is involved in cotton response to salt stress*, *BMC Plant Biol.*, 2019, vol. 19, pp. 459. <https://doi.org/10.1186/s12870-019-2088-0>
- Zhao, L., Wang, S., Fu, Y.-B., and Wang, H., *Arabidopsis seed stored mRNAs are degraded constantly over aging time, as revealed by new quantification methods*, *Front Plant Sci.*, 2020, vol. 10. <https://doi.org/10.3389/fpls.2019.01764>
- Zhao, M., Yang, S., Liu, X., and Wu, K., *Arabidopsis histone demethylases LDL1 and LDL2 control primary seed dormancy by regulating delay of germination 1 and ABA signaling-related genes*, *Front. Plant Sci.*, 2015, vol. 6, pp. 159. <https://doi.org/10.3389/fpls.2015.00159>
- Zhao, X., Dou, L., Gong, Z., Wang, X., and Mao, T., *BES1 hinders abscisic acid insensitive 5 and promotes seed germination in Arabidopsis*, *New Phytologist*, 2019, vol. 221, no. 2, pp. 908–918. <https://doi.org/10.1111/nph.15422>
- Zhou, S., Huang, K., Zhou, Y., et al., *Degradome sequencing reveals an integrative miRNA-mediated gene interaction network regulating rice seed vigor*, *BMC Plant Biol.*, 2022, vol. 22, pp. 269. <https://doi.org/10.1186/s12870-022-03645-2>
- Zhou, Y., Zhou, S.Q., Wang, L.P., Wu, D., Cheng, H.L., Du, X., et al., *miR164c and miR168a regulate seed vigor in rice*, *J. Integr. Plant Biol.*, 2020, vol. 62, pp. 470–486. <https://doi.org/10.1111/jipb.12792>
- Zinsmeister, J., Berriri, S., Basso, D.P., Ly-Vu, B., Dang, T., Lalanne, D., Da Silva, E.A.A., Leprince, O., and Buitink, J., *The seed-specific Heat Shock Factor A9 regulates the depth of dormancy in Medicago truncatula ABA signalling*, *Plant, Cell & Environment*, 2020, vol. 43(11), pp. 2508–2522. <https://doi.org/10.1111/pce.13828>
- Zinsmeister, J., Lalanne, D., Ly Vu, B., Schoefs, B., Marchand, J., Dang, T.T., Buitink, J., and Leprince, O., *Absciscic Acid Insensitive 4 coordinates eoplast formation to ensure acquisition of seed longevity during maturation in Medicago truncatula*, *Plant J.*, 2023, vol. 113(5), pp. 934–953. <https://doi.org/10.1111/tpj.16091>
- Zinsmeister, J., Lalanne, D., Terrasson, E., Chatelain, E., Vandecasteele, C., Vu, B.L., Dubois-Laurent, C., Geoffriau, E., Signor, C.L., and Dalmais, M., *ABI5 is a regulator of seed maturation and longevity in legumes*, *Plant Cell*, 2016, vol. 28(10), pp. 2735–2754. <https://doi.org/10.1105/tpc.16.00337>
- Zuo, J.H., Chen, F.Y., Li, X.Y., Xia, X.C., Cao, H., Liu, J.D., and Liu, Y.X., *Genome-wide association study reveals loci associated with seed longevity in common wheat (Triticum aestivum L.)*, *Plant Breed.*, 2020, vol. 139, pp. 295–303. <https://doi.org/10.1111/pbr.12784>

Received February 26, 2024

Received June 10, 2025

Accepted January 18, 2026