



UvA-DARE (Digital Academic Repository)

Genomic regions under selection in crop-wild hybrids of lettuce: implications for crop breeding and environmental risk assessment

Hartman, Y.

Publication date
2012

[Link to publication](#)

Citation for published version (APA):

Hartman, Y. (2012). *Genomic regions under selection in crop-wild hybrids of lettuce: implications for crop breeding and environmental risk assessment*. [Thesis, fully internal, Universiteit van Amsterdam].

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

R

References

References

- Abramoff, M. D., P. J. Magalhaes, and S. J. Ram. 2004. Image processing with ImageJ. *Biophotonics International* **11**:36–42.
- ACRE. 2007. Managing the footprint of agriculture: towards a comparative assessment of risks and benefits for novel agricultural systems. Report of the ACRE Sub-Group on Wider Issues raised by the Farm-Scale Evaluations of Herbicide Tolerant GM Crops. URL: <http://webarchive.nationalarchives.gov.uk/20080727101330/http://www.defra.gov.uk/environment/acre/fsewiderissues/pdf/acre-wi-final.pdf>
- Al-Ahmad, H., S. Galili, and J. Gressel. 2004. Tandem constructs to mitigate transgene persistence: tobacco as a model. *Molecular Ecology* **13**:697–710.
- Al-Ahmad, H., S. Galili, and J. Gressel. 2005. Poor competitive fitness of transgenically mitigated tobacco in competition with the wild type in a replacement series. *Planta* **222**:372–385.
- Andow, D. A., and C. Zwahlen. 2006. Assessing environmental risks of transgenic plants. *Ecology Letters* **9**:196–214.
- Argyris, J., M. J. Truco, O. Ochoa, S. J. Knapp, D. W. Still, G. M. Lenssen, J. W. Schut, R. W. Michelmore, and K. J. Bradford. 2005. Quantitative trait loci associated with seed and seedling traits in *Lactuca*. *Theoretical and Applied Genetics* **111**:1365–1376.
- Armstrong, T. T., R. G. Fitzjohn, L. E. Newstrom, A. D. Wilton, and W. G. Lee. 2005. Transgene escape: what potential for crop–wild hybridization? *Molecular Ecology* **14**:2111–2132.
- Baack, E. J., Y. Sapir, M. A. Chapman, J. M. Burke, and L. H. Rieseberg. 2008. Selection on domestication traits and quantitative trait loci in crop–wild sunflower hybrids. *Molecular Ecology* **17**:666–677.
- Barton, N. H. 2001. The role of hybridization in evolution. *Molecular Ecology* **10**:551–568.
- Beavis, W. 1998. QTL Analyses: Power, Precision and Accuracy. Pages 145–162 in A. H. Paterson, ed. *Molecular Dissection of Complex Trait*. CRC Press, Boca Raton.
- Beckie, H. J., and M. D. K. Owen. 2007. Herbicide-resistant crops as weeds in North America. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* **2**: No. 44. doi: 10.1079/PAVSNNR20072044.
- Bhatnagar-Mathur, P., V. Vadez, and K. K. Sharma. 2008. Transgenic approaches for abiotic stress tolerance in plants: retrospect and prospects. *Plant Cell Reports* **27**:411–424.
- Bijlsma, R., M. D. D. Westerhof, L. P. Roekx, and I. Pen. 2010. Dynamics of genetic rescue in inbred *Drosophila melanogaster* populations. *Conservation Genetics* **11**:449–462.
- Burger, J. C., M. A. Chapman, and J. M. Burke. 2008. Molecular insights into the evolution of crop plants. *American Journal of Botany* **95**:113–122.
- Burke, J. M., and M. L. Arnold. 2001. Genetics and the fitness of hybrids. *Annual Review of Genetics* **35**:31–52.
- Burke, J. M., S. Tang, S. J. Knapp, and L. H. Rieseberg. 2002. Genetic analysis of sunflower domestication. *Genetics* **161**:1257–1267.
- Burke J. M., J. C. Burger, and M. A. Chapman. 2007. Crop evolution: from genetics to genomics. *Current Opinion in Genetics and Development* **17**:525–532.
- Cai, H. W., and H. Morishima. 2002. QTL clusters reflect character associations in wild and cultivated rice. *Theoretical and Applied Genetics* **104**:1217–1228.
- Campbell, L. G., A. A. Snow, and C. E. Ridley. 2006. Weed evolution after crop gene introgression: greater survival and fecundity of hybrids in a new environment. *Ecology Letters* **9**:1198–1209.
- Campbell, L. G., and A. A. Snow. 2007. Competition alters life history and increases the relative fecundity of crop–wild radish hybrids (*Raphanus* spp.). *New Phytologist* **173**:648–660.
- Campbell, L. G., A. A. Snow, P. M. Sweeney, and J. M. Ketner. 2009. Rapid evolution in crop–weed hybrids under artificial selection for divergent life histories. *Evolutionary*

- Applications **2**:172–186.
- Campos, H., A. Cooper, J. E. Habben, G. O. Edmeades, J. R. Schussler. 2004. Improving drought tolerance in maize: a view from industry. *Field Crops Research* **90**:19–34.
- Cao, Q. J., H. Xia, X. Yang, and B. R. Lu. 2009. Performance of Hybrids between Weedy Rice and Insect-resistant Transgenic Rice under Field Experiments: Implication for Environmental Biosafety Assessment. *Journal of Integrative Plant Biology* **51**:1138–1148.
- Chahal, G. S., and S. S. Gosal. 2002. Principles and procedures of plant breeding: biotechnological and conventional approaches. Alpha Science International Ltd., Harrow, UK.
- Chapman, M. A., and J. M. Burke. 2006. Letting the gene out of the bottle: the population genetics of genetically modified crops. *New Phytologist* **170**:429–443.
- Chiang, G. C. K., D. Barua, E. M. Kramer, R. M. Amasino, and K. Donohue. 2009. Major flowering time gene, flowering locus C, regulates seed germination in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences USA* **106**:11661–11666.
- Churchill, G. A., and R. W. Doerge. 1994. Empirical threshold values for quantitative mapping. *Genetics* **138**:963–971.
- Collard, B. C. Y., M. Z. Z. Jahufe, J. B. Brouwe, and E. C. K. Pang. 2005. An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: The basic concepts. *Euphytica* **142**:169–196.
- Collard, B. C. Y., and D. J. Mackill. 2008. Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. *Philosophical Transactions of the Royal Society B* **363**:557–572.
- Collins, N. C., F. Tardieu, and R. Tuberosa. 2008. Quantitative trait loci and crop performance under abiotic stress: Where do we stand? *Plant Physiology* **147**:469–486.
- Cominelli, E., and C. Tonelli. 2010. Transgenic crops coping with water scarcity. *New Biotechnology* **27**:473–477.
- Craig, W., M. Tepfer, G. Degrassi, and D. Ripandelli. 2008. An overview of general features of risk assessments of genetically modified crops. *Euphytica* **164**:853–880.
- Cuartero, J., M. C. Bolarin, M. J. Asins, and V. Moreno. 2006. Increasing salt tolerance in the tomato. *Journal of Experimental Botany* **57**:1045–1058.
- D’Andrea, L., F. Felber, and R. Guadagnuolo. 2008. Hybridization rates between lettuce (*Lactuca sativa*) and its wild relative (*L. serriola*) under field conditions. *Environmental Biosafety Research* **7**:61–71.
- D’Andrea, L., O. Broennimann, G. Kozłowski, A. Guisan, X. Morin, J. Keller-Senften, and F. Felber. 2009. Climate change, anthropogenic disturbance and the northward range expansion of *Lactuca serriola* (Asteraceae). *Journal of Biogeography* **36**:1573–1587.
- Dale, P. J. 1999. Public concerns over transgenic crops. *Genome Research* **9**:1159–1162.
- Danan, S., J.-B. Veyrieras, and V. Lefebvre. 2011. Construction of a potato consensus map and QTL meta-analysis offer new insights into the genetic architecture of late blight resistance and plant maturity traits. *BMC Plant Biology* **11**:16.
- Dechaine, J. M., J. C. Burger, M. A. Chapman, G. J. Seiler, R. Brunick, S. J. Knapp, and J. M. Burke. 2009. Fitness effects and genetic architecture of plant–herbivore interactions in sunflower crop–wild hybrids. *New Phytologist* **184**:828–841.
- Dempewolf, H., L. H. Rieseberg, and Q. C. Cronk. 2008. Crop domestication in the Compositae: a family-wide trait assessment. *Genetic Resources and Crop Evolution* **55**:1141–1157.
- DeVicente, M. C., and S. D. Tanksley. 1993. QTL analysis of transgressive segregation in an interspecific tomato cross. *Genetics* **134**:585–596.
- De Vries, I. M. 1990. Crossing experiments of Lettuce cultivars and species (*Lactuca* sect *Lactuca*, Compositae). *Plant Systematics and Evolution* **171**:233–248.

References

- De Vries, I. M. 1997. Origin and domestication of *Lactuca sativa* L. *Genetic Resources and Crop Evolution* **44**:165–174.
- Doebley, J., and A. Stec. 1993. Inheritance of the morphological differences between maize and teosinte – comparison of results for two F₂ populations. *Genetics* **134**:559–570.
- Doerge, R. W., and G. A. Churchill. 1996. Permutation tests for multiple loci affecting a quantitative character. *Genetics* **142**:285–294.
- Doganlar, S., A. Frary, M. C. Daunay, R. N. Lester, and S. D. Tanksley. 2002. Conservation of gene function in the Solanaceae as revealed by comparative mapping of domestication traits in eggplant. *Genetics* **161**:1713–1726.
- EFSA. 2011. Guidance for risk assessment of food and feed from genetically modified plants. *EFSA Journal* **9**:2150.
- Ellstrand, N. C. 2003. *Dangerous Liaisons? When Cultivated Plants Mate with their Wild Relatives*. John Hopkins University Press, Baltimore, Maryland.
- Ellstrand, N. C., S. M. Heredia, J. A. Leak-Garcia, J. M. Heraty, J. C. Burger, L. Yao, S. Nohzadeh-Malakshah, and C. E. Ridley. 2011. Crops gone wild: evolution of weeds and invasives from domesticated ancestors. *Evolutionary Applications* **3**:494–504.
- Ellstrand, N. C. In press. Over a decade of crop transgenes out-of-place. In C. A. Wozniak and C. W. A. McHughen, eds. *Regulation of Agricultural Biotechnology: The United States and Canada*. Springer, New York.
- Erickson, D. L., C. B. Fenster, H. K. Stenoien, and D. Price. 2004. Quantitative trait locus analyses and the study of evolutionary process. *Molecular Ecology* **13**:2505–2522.
- Fakheran, S., C. Paul-Victor, C. Heichinger, B. Schmid, U. Grossniklaus, and L. A. Turnbull. 2010. Adaptation and extinction in experimentally fragmented landscapes. *Proceedings of the National Academy of Sciences USA* **107**:19120–19125.
- Flint-Garcia, S. A., J. M. Thornsberry, and E. S. Buckler. 2003. Structure of linkage disequilibrium in plants. *Annual Review of Plant Biology* **54**:357–374.
- Frary, A., T. C. Nesbitt, S. Grandillo, E. van der Knaap, B. Cong, J. P. Liu, J. Meller, R. Elber, K. B. Alpert, and S. D. Tanksley. 2000. fw2.2: A quantitative trait locus key to the evolution of tomato fruit size. *Science* **289**:85–88.
- Gallardo, M., L. E. Jackson, and R. B. Thompson. 1996. Shoot and root physiological responses to localized zones of soil moisture in cultivated and wild lettuce (*Lactuca* spp). *Plant Cell and Environment* **19**:1169–1178.
- Gardner, K. M., and R. G. Latta. 2006. Identifying loci under selection across contrasting environments in *Avena barbata* using quantitative trait locus mapping. *Molecular Ecology* **15**:1321–1333.
- Gardner, K. M., and R. G. Latta. 2008. Heritable variation and genetic correlation of quantitative traits within and between ecotypes of *Avena barbata*. *Journal of Evolutionary Biology* **21**:737–748.
- Giannino, D., C. Nicolodi, G. Testone, E. Di Giacomo, M. A. Iannelli, G. Frugis, and D. Mariotti. 2008. Pollen-mediated transgene flow in lettuce (*Lactuca sativa* L.). *Plant Breeding* **127**:308–314.
- Gressel, J. 1999. Tandem constructs: preventing the rise of superweeds. *Trends in Biotechnology* **17**:361–366.
- Gross, B. L., and K. M. Olsen. 2010. Genetic perspectives on crop domestication. *Trends in Plant Science* **15**:529–537.
- Hails, R. S., and K. Morley. 2005. Genes invading new populations: a risk assessment perspective. *Trends in Ecology and Evolution* **20**:245–252.
- Halfhill, M. D., J. P. Sutherland, H. S. Moon, G. M. Poppy, S. I. Warwick, A. K. Weissinger, T. W. Rufty, P. L. Raymer, and C. N. Stewart. 2005. Growth, productivity, and competitiveness

- of introgressed weedy *Brassica rapa* hybrids selected for the presence of Bt cry1Ac and gfp transgenes. *Molecular Ecology* **14**:3177–3189.
- Halpin, C. 2005. Gene stacking in transgenic plants – the challenge for 21st century plant biotechnology. *Plant Biotechnology Journal* **3**:141–155.
- Hancock, J. F. 2005. Contributions of domesticated plant studies to our understanding of plant evolution. *Annals of Botany* **96**:953–963.
- Harlan, J. R. 1992. *Crops and man*. American Society of Agronomy, Madison, Wisconsin, USA
- Hartman, Y., D. A. P. Hooftman, B. Uwimana, C. C. M. van de Wiel, M. J. M. Smulders, R. G. F. Visser, and P. H. van Tienderen. 2012. Genomic regions in crop–wild hybrids of lettuce are affected differently in different environments: implications for crop breeding. Evolutionary applications (in press). doi: 10.1111/j.1752-4571.2012.00240.x.
- Hauser, T. P., R. B. Jorgensen, and H. Ostergard. 1998a. Fitness of backcross and F-2 hybrids between weedy *Brassica rapa* and oilseed rape (*B. napus*). *Heredity* **81**:436–443.
- Hauser, T. P., R. G. Shaw, and H. Ostergard. 1998b. Fitness of F-1 hybrids between weedy *Brassica rapa* and oilseed rape (*B. napus*). *Heredity* **81**:429–435.
- Haygood, R., A. R. Ives, and D. A. Andow. 2004. Population genetics of transgene containment. *Ecology Letters* **7**:213–220.
- Hedge, S. B., J. D. Nason, J. M. Clegg, and N. C. Ellstrand. 2006. The evolution of California's wild radish has resulted in the extinction of its progenitors. *Evolution* **60**:1187–1197.
- Hedgecock, D., D. J. McGoldrick, and B. L. Bayne. 1995. Hybrid vigor in Pacific oysters: An experimental approach using crosses among inbred lines. *Aquaculture* **137**:285–298.
- Hooftman, D. A. P., J. G. B. Oostermeijer, M. M. J. Jacobs, and H. C. M. Den Nijs. 2005. Demographic vital rates determine the performance advantage of crop–wild hybrids in lettuce. *Journal of Applied Ecology* **42**:1086–1095.
- Hooftman, D. A. P., J. G. B. Oostermeijer, and J. C. M. den Nijs. 2006. Invasive behaviour of *Lactuca serriola* (Asteraceae) in the Netherlands: Spatial distribution and ecological amplitude. *Basic and Applied Ecology* **7**:507–519.
- Hooftman, D. A. P., M. J. D. Jong, J. G. B. Oostermeijer, and H. C. M. Den Nijs. 2007. Modelling the long-term consequences of crop–wild relative hybridization: a case study using four generations of hybrids. *Journal of Applied Ecology* **44**:1035–1045.
- Hooftman, D. A. P., Y. Hartman, J. G. B. Oostermeijer, and H. C. M. Den Nijs. 2009. Existence of vigorous lineages of crop–wild hybrids in Lettuce under field conditions. *Environmental Biosafety Research* **8**:203–217.
- Hooftman, D. A. P., A. J. Flavell, H. Jansen, H. C. M. den Nijs, N. H. Syed, A. P. Sørensen, P. Orozco-ter Wengel, and C. C. M. van de Wiel. 2011. Locus-dependent selection in crop–wild hybrids of lettuce under field conditions and its implication for GM crop development. *Evolutionary Applications* **4**:648–659.
- Huangfu, C., S. Qiang, and X. Song. 2011. Performance of hybrids between transgenic oilseed rape (*Brassica napus*) and wild *Brassica juncea*. An evaluation of potential for transgene escape. *Crop Protection* **30**:57–62.
- Hund, A., R. Reimer, and R. Messmer. 2011. A consensus map of QTLs controlling the root length of maize. *Plant and Soil* **344**:143–158.
- Huxel, G. R. 1999. Rapid displacement of native species by invasive species: effects of hybridization. *Biological Conservation* **89**:143–152.
- Hyne, V., M. J. Kearsey, D. J. Pike, and J. W. Snape. 1995. QTL analysis – unreliability and bias in estimation procedures. *Molecular Breeding* **1**:273–282.
- Isemura, T., A. Kaga, N. Tomooka, T. Shimizu, and D. A. Vaughan. 2010. The genetics of domestication of rice bean, *Vigna umbellata*. *Annals of Botany* **106**:927–944.
- Jackson, L. E. 1995. Root architecture in cultivated and wild lettuce (*Lactuca* spp.). *Plant, Cell*

References

- and Environment **18**:885–894.
- James, C. 2010. Global Status of Commercialized Biotech/GM Crops: 2010. ISAAA Brief No. **42**. ISAAA: Ithaca, NY.
- Johansen-Morris, A. D., and R. G. Latta. 2006. Fitness consequences of hybridization between ecotypes of *Avena barbata*: Hybrid breakdown, hybrid vigor, and transgressive segregation. *Evolution* **60**:1585–1595.
- Johansen-Morris, A. D., and R. G. Latta. 2008. Genotype by environment interactions for fitness in hybrid genotypes of *Avena barbata*. *Evolution* **62**:573–585.
- Johnson, W. C., L. E. Jackson, O. Ochoa, R. van Wijk, J. Peleman, D. A. St Clair, and R. W. Michelmore. 2000. Lettuce, a shallow-rooted crop, and *Lactuca serriola*, its wild progenitor, differ at QTL determining root architecture and deep soil water exploitation. *Theoretical and Applied Genetics* **101**:1066–1073.
- Kaga, A., T. Isemura, N. Tomooka, and D. A. Vaughan. 2008. The genetics of domestication of the azuki bean (*Vigna angulatis*). *Genetics* **178**:1013–1036.
- Kesseli, R. V., O. Ochoa and R. W. Michelmore. 1991. Variation at RFLP loci in *Lactuca* spp. and the origin of cultivated lettuce (*L. sativa*). *Genome* **34**:430–436.
- Knight, H., and M. R. Knight. 2001. Abiotic stress signalling pathways: specificity and cross-talk. *Trends in Plant Science* **6**:262–267.
- Koinange, E. M. K., S. P. Singh, and P. Gepts. 1996. Genetic control of the domestication syndrome in common bean. *Crop Science* **36**:1037–1045.
- Koopman, W. J. M., M. J. Zevenbergen, and R. G. Van den Berg. 2001. Species relationships in *Lactuca* SL (Lactuceae, Asteraceae) inferred from AFLP fingerprints. *American Journal of Botany* **88**:1881–1887.
- Krieger, U., Z. B. Lippman, and D. Zamir. 2010. The flowering gene single flower truss drives heterosis for yield in tomato. *Nature Genetics* **42**:459–U138.
- Kwit, C., H. S. Moon, S. I. Warwick, and C. N. Stewart. 2011. Transgene introgression in crop relatives: molecular evidence and mitigation strategies. *Trends in Biotechnology* **29**:284–293.
- Latta, R. G., K. M. Gardner, and A. D. Johansen-Morris. 2007. Hybridization, recombination, and the genetic basis of fitness variation across environments in *Avena barbata*. *Genetica* **129**:167–177.
- Latta, R. G., K. M. Gardner, and D. A. Staples. 2010. Quantitative Trait Locus Mapping of Genes Under Selection Across Multiple Years and Sites in *Avena barbata*: Epistasis, Pleiotropy, and Genotype-by-Environment Interactions. *Genetics* **185**:375–385.
- Lebeda, A., I. Dolezalova, E. Kristkova, and B. Mieslerova. 2001. Biodiversity and ecogeography of wild *Lactuca* spp. in some European countries. *Genetic Resources and Crop Evolution* **48**:153–164.
- Lebeda, A., I. Dolezalova, E. Kristkova, M. Kitner, I. Petzelova, B. Mieslerova, and A. Novotna. 2009. Wild *Lactuca* germplasm for lettuce breeding: current status, gaps and challenges. *Euphytica* **170**:15–34.
- Lee, D., and E. Natesan. 2006. Evaluating genetic containment strategies for transgenic plants. *Trends in Biotechnology* **24**:109–114.
- Lexer, C., M. E. Welch, O. Raymond, and L. H. Rieseberg. 2003. The origin of ecological divergence in *Helianthus paradoxus* (Asteraceae): Selection on transgressive characters in a novel hybrid habitat. *Evolution* **57**:1989–2000.
- Linder, C. R., I. Taha, G. J. Seiler, A. A. Snow, and L. H. Rieseberg. 1998. Long-term introgression of crop genes into wild sunflower populations. *Theoretical and Applied Genetics* **96**:339–347.
- Lombardo A., D. Cesana, P. Genovese, B. Di Stefano, E. Provasi, D. F. Colombo, M. Neri, Z.

- Magnani, A. Cantore, P. Lo Riso, et al. 2011. Site-specific integration and tailoring of cassette design for sustainable gene transfer. *Nature Methods* **8**:861–U135.
- Lynch, M., and B. Walsh. 1998. *Genetics and Analysis of Quantitative Traits*. pp 663–665. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, USA.
- Malmberg, R. L., S. Held, A. Waits, and R. Mauricio. 2005. Epistasis for fitness-related quantitative traits in *Arabidopsis thaliana* grown in the field and in the greenhouse. *Genetics* **171**:2013–2027.
- Martin, N. H., A. C. Bouck, and M. L. Arnold. 2006. Detecting adaptive trait introgression between *Iris fulva* and *I. brevicaulis* in highly selective field conditions. *Genetics* **172**:2481–2489.
- Mathews, K. L., M. Malosetti, S. Chapman, L. McIntyre, M. Reynolds, R. Shorter, and F. van Eeuwijk. 2008. Multi-environment QTL mixed models for drought stress adaptation in wheat. *Theoretical and Applied Genetics* **117**:1077–1091.
- Mauricio, R. 2001. Mapping quantitative trait loci in plants: Uses and caveats for evolutionary biology. *Nature Reviews Genetics* **2**:370–381.
- Mercer, K. L., D. L. Wyse, and R. G. Shaw. 2006. Effects of competition on the fitness of wild and crop–wild hybrid sunflower from a diversity of wild populations and crop lines. *Evolution* **60**:2044–2055.
- Mercer, K. L., D. A. Andow, D. L. Wyse, and R. G. Shaw. 2007. Stress and domestication traits increase the relative fitness of crop–wild hybrids in sunflower. *Ecology Letters* **10**:383–393.
- Mittler, R., and E. Blumwald. 2010. Genetic Engineering for Modern Agriculture: Challenges and Perspectives. *Annual Review of Plant Biology* **61**:443–462.
- Morjan, C. L., and L. H. Rieseberg. 2004. How species evolve collectively: implications of gene flow and selection for the spread of advantageous alleles. *Molecular Ecology* **13**:1341–1356.
- Muraya, M. M., H. H. Geiger, F. Sagnard, L. Toure, P. C. S. Traore, S. Togola, S. de Villiers, and H. K. Parzies. 2012. Adaptive values of wild x cultivated sorghum (*Sorghum bicolor* (L.) Moench) hybrids in generations F(1), F(2), and F(3). *Genetic Resources and Crop Evolution* **59**:83–93.
- Nagata, R. T. 1992. Clip-and-wash method of emasculation for lettuce. *Hortiscience* **27**:907–908.
- Nandy, S., and V. Srivastava. 2011. Site-specific gene integration in rice genome mediated by the FLP-FRT recombination system. *Plant Biotechnology Journal* **9**:713–721.
- Park, B. J., Z. C. Liu, A. Kanno, and T. Kameya. 2005. Increased tolerance to salt- and water-deficit stress in transgenic lettuce (*Lactuca sativa* L.) by constitutive expression of LEA. *Plant Growth Regulation* **45**:165–171.
- Pilson, D., and H. R. Prendeville. 2004. Ecological effects of transgenic crops and the escape of transgenes into wild populations. *Annual Review of Ecology, Evolution and Systematics* **35**:149–174.
- Poncet, V., F. Lamy, K. M. Devos, M. D. Gale, A. Sarr, and T. Robert. 2000. Genetic control of domestication traits in pearl millet (*Pennisetum glaucum* L., Poaceae). *Theoretical and Applied Genetics* **100**:147–159.
- Prince, S. D., and R. N. Carter. 1977. Prickly lettuce (*Lactuca serriola* L.) in Britain. *Watsonia* **11**:331–338.
- Prudent, M., M. Causse, M. Genard, P. Tripodi, S. Grandillo, and N. Bertin. 2009. Genetic and physiological analysis of tomato fruit weight and composition: influence of carbon availability on QTL detection. *Journal of Experimental Botany* **60**:923–937.
- Purugganan, M. D., and D. Q. Fuller. 2009. The nature of selection during plant domestication.

References

- Nature **457**:843–848.
- R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Rhode, J. M., and M. B. Cruzan. 2005. Contributions of heterosis and epistasis to hybrid fitness. *American Naturalist* **166**:124–139.
- Rieseberg, L. H., M. A. Archer, and R. K. Wayne. 1999. Transgressive segregation, adaptation and speciation. *Heredity* **83**:363–372.
- Rieseberg, L. H., S. J. E. Baird, and K. A. Gardner. 2000. Hybridization, introgression, and linkage evolution. *Plant Molecular Biology* **42**:205–224.
- Rieseberg, L. H., A. Widmer, A. M. Arntz, and J. M. Burke. 2002. Directional selection is the primary cause of phenotypic diversification. *Proceedings of the National Academy of Sciences, USA* **99**:12242–12245.
- Rieseberg, L. H., A. Widmer, A. M. Arntz, and J. M. Burke. 2003. The genetic architecture necessary for transgressive segregation is common in both natural and domesticated populations. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* **358**:1141–1147.
- Rieseberg, L. H., S. C. Kim, R. A. Randell, K. D. Whitney, B. L. Gross, C. Lexer, and K. Clay. 2007. Hybridization and the colonization of novel habitats by annual sunflowers. *Genetica* **129**:149–165.
- Romeis, J., N. C. Lawo, and A. Raybould. 2009. Making effective use of existing data for case-by-case risk assessments of genetically engineered crops. *Journal of Applied Entomology* **133**:571–583.
- Rose, C. W., R. J. Millwood, H. S. Moon, M. R. Rao, M. D. Halfhill, P. L. Raymer, S. I. Warwick, H. Al-Ahmad, J. Gressel, and C. N. Stewart. 2009. Genetic load and transgenic mitigating genes in transgenic *Brassica rapa* (field mustard) x *Brassica napus* (oilseed rape) hybrid populations. *BMC Biotechnology* **9**:93.
- Ross-Ibarra, J. 2005. Quantitative trait loci and the study of plant domestication. *Genetica* **123**:197–204.
- Roy, S. J., E. J. Tucker, and M. Tester. 2011. Genetic analysis of abiotic stress tolerance in crops. *Current Opinion in Plant Biology* **14**:232–239.
- Ryder, E. J. 1999. Lettuce, Endive and Chicory. CAB International, Wallingford, UK.
- Ryder, E. J., and T. W. Whitaker. 1976. Lettuce. In *Evolution of Crop Plants*. Ed. N.W. Sommonds Longman. Pp. 39–41.
- Scascitelli, M., K. D. Whitney, R. A. Randell, M. King, C. A. Buerkle, and L. H. Rieseberg. 2010. Genome scan of hybridizing sunflowers from Texas (*Helianthus annuus* and *H. debilis*) reveals asymmetric patterns of introgression and small islands of genomic differentiation. *Molecular Ecology* **19**:521–541.
- Schierenbeck, K. A., and N. C. Ellstrand. 2009. Hybridization and the evolution of invasiveness in plants and other organisms. *Biological Invasions* **11**:1093–1105.
- Shukla, V. K., Y. Doyon, J. C. Miller, R. C. DeKolver, E. A. Moehle, S. E. Worden, J. C. Mitchell, N. L. Arnold, S. Gopalan, X. Meng, et al. 2009. Precise genome modification in the crop species *Zea mays* using zinc-finger nucleases. *Nature* **459**:437–441.
- Simonne, A., E. Simonne, R. Eitenmiller, and C. H. Coker. 2002. Bitterness and composition of lettuce varieties grown in the southeastern United States. *HortTechnology* **12**:721–726.
- Snow, A. A., P. Moran-Palma, L. H. Rieseberg, A. Wszelaki, and G. J. Seiler. 1998. Fecundity, phenology, and seed dormancy of F-1 wild-crop hybrids in sunflower (*Helianthus annuus*, Asteraceae). *American Journal of Botany* **85**:794–801.
- Snow, A. A., D. A. Andow, P. Gepts, E. M. Hallerman, A. Power, J. M. Tiedje, and L. L.

- Wolfenbarger. 2005. Genetically engineered organisms and the environment: Current status and recommendations. *Ecological Applications* **15**:377–404.
- Snow, A. A., T. M. Culley, L. G. Campbell, P. M. Sweeney, S. G. Hegde, and N. C. Ellstrand. 2010. Long-term persistence of crop alleles in weedy populations of wild radish (*Raphanus raphanistrum*). *New Phytologist* **186**:537–548.
- SPSS Inc. 2009. PASW Statistics 17.0 Command Syntax Reference. SPSS Inc., Chicago
- Stewart, C. N., M. D. Halfhill, and S. I. Warwick. 2003. Transgene introgression from genetically modified crops to their wild relatives. *Nature Reviews Genetics* **4**:806–817.
- Swamy, B. P. M., and N. Sarla. 2011. Meta-analysis of yield QTLs derived from inter-specific crosses of rice reveals consensus regions and candidate genes. *Plant Molecular Biology Reporter* **29**:663–680.
- Thiemann, A., S. Meyer, and S. Scholten. 2009. Heterosis in plants: Manifestation in early seed development and prediction approaches to assist hybrid breeding. *Chinese Science Bulletin* **54**:2363–2375.
- Tilman, D., C. Balzer, J. Hill, and B. L. Befort. 2011. Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences USA* **108**:20260–20264.
- United Nations, Department of Economic and Social Affairs, Population Division. 2011. *World Population Prospects: The 2010 Revision, Highlights and Advanced Tables*. ESA/P/WP.220.
- Uwimana, B. 2011. A genetic analysis of the introgression process from cultivated lettuce (*Lactuca sativa* L.) to wild prickly lettuce (*L. serriola* L.). PhD thesis, Wageningen University, the Netherlands.
- Uwimana, B., L. D'Andrea, F. Felber, D. A. P. Hooftman, H. C. M. den Nijs, M. J. M. Smulders, R. G. F. Visser, and C. C. M. van de Wiel. 2012a. A Bayesian analysis of gene flow from crops to their wild relatives: cultivated (*Lactuca sativa* L.) and prickly lettuce (*L. serriola* L.) and the recent expansion of *L. serriola* in Europe. *Molecular Ecology* (in press). doi: 10.1111/j.1365-294X.2012.05489.x
- Uwimana, B., M. J. M. Smulders, D. A. P. Hooftman, Y. Hartman, P. H. van Tienderen, J. Jansen, L. K. McHale, R. W. Michelmore, R. G. F. Visser, and C. C. M. van de Wiel. 2012b. Crop to wild introgression in lettuce: following the fate of crop genome segments in backcross populations. *BMC Plant Biology* **12**:43
- Van de Wiel, C. C. M., T. S. Rajičić, R. van Treuren, K. J. Dehmer, C. G. van der Linden, and T. J. L. Van Hintum. 2010. Distribution of genetic diversity in wild European populations of prickly lettuce (*Lactuca serriola*): implications for plant genetic resources management. *Plant Genetic Resources-Characterization and Utilization* **8**:171–181.
- van der Meijden, R. 1996. *Heukels Flora van Nederland*. Wolters-Noordhoff, Groningen, the Netherlands.
- Vaughan, D. A., E. Balazs, and J. S. Heslop-Harrison. 2007. From crop domestication to super-domestication. *Annals of Botany* **100**:893–901.
- Vinocur, B., and A. Altman. 2005. Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. *Current Opinion in Biotechnology* **16**:123–132.
- Vision, T. J., D. G. Brown, D. B. Shmoys, R. T. Durrett, and S. D. Tanksley. 2000. Selective mapping: A strategy for optimizing the construction of high-density linkage maps. *Genetics* **155**:407–420.
- Visscher, P. M., W. G. Hill, and N. R. Wray. 2008. Heritability in the genomics era – concepts and misconceptions. *Nature Reviews Genetics* **9**: 255–266.
- Voorrips, R. E. 2002. MapChart: Software for the graphical presentation of linkage maps and QTLs. *Journal of Heredity* **93**:77–78.

References

- Wang, S., C. J. Basten, and Z.-B. Zeng. 2010. Windows QTL Cartographer 2.5. Department of Statistics, North Carolina State University, Raleigh, NC.
- Wang, W. X., B. Vinocur, and A. Altman. 2003. Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta* **218**:1–14.
- Warwick, S. I., A. Legere, M. J. Simard, and T. James. 2008. Do escaped transgenes persist in nature? The case of an herbicide resistance transgene in a weedy *Brassica rapa* population. *Molecular Ecology* **17**:1387–1395.
- Warwick, S. I., H. J. Beckie, and L. M. Hall. 2009. Gene Flow, Invasiveness, and Ecological Impact of Genetically Modified Crops. *The Year in Evolutionary Biology 2009* **1168**:72–99.
- Weinig, C., M. C. Ungerer, L. A. Dorn, N. C. Kane, Y. Toyonaga, S. S. Halldorsdottir, T. F. C. Mackay, M. D. Purugganan, and J. Schmitt. 2002. Novel loci control variation in reproductive timing in *Arabidopsis thaliana* in natural environments. *Genetics* **162**:1875–1884.
- Weinig, C., L. A. Dorn, N. C. Kane, Z. M. German, S. S. Hahdorsdottir, M. C. Ungerer, Y. Toyonaga, T. F. C. Mackay, M. D. Purugganan, and J. Schmitt. 2003. Heterogeneous selection at specific loci in natural environments in *Arabidopsis thaliana*. *Genetics* **165**:321–329.
- Wills, D. M., and J. M. Burke. 2007. Quantitative trait locus analysis of the early domestication of sunflower. *Genetics* **176**:2589–2599.
- Witcombe, J. R., P. A. Hollington, C. J. Howarth, S. Reader, and K. A. Steele. 2008. Breeding for abiotic stresses for sustainable agriculture. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**:703–716.
- Zhang, F. Z., C. Wagstaff, A. M. Rae, A. K. Sihota, C. W. Keevil, S. D. Rothwell, G. J. J. Clarkson, R. W. Michelmore, M. J. Truco, M. S. Dixon, and G. Taylor. 2007. QTLs for shelf life in lettuce co-locate with those for leaf biophysical properties but not with those for leaf developmental traits. *Journal of Experimental Botany* **58**:1433–1449.