

3502-470 Plant Genetic Resources

Prof. Karl Schmid SS 2025

Institute of Plant Breeding, Seed Science and Population Genetics University of Hohenheim

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Recapitulation

- Strong phenotypic changes during domestication.
- \cdot Successful identification of domestication genes.
- \cdot teosinte branched 1 (tb1) in maize is well characterized.
- *tb1*: Additional expression domains in maize; repression of lateral shoots.
- \cdot Change in expression is caused by mutations in regulatory region.
- \cdot Transposable elements mostly responsible for the change.

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Outline

- 1. Domestication syndrome
- 2. Mapping of genes controlling domestication traits
- 3. Population genetics of domestication

Searching for genes that experience selection

Analysis of domestication selection in maize

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Types of genes evolving under artificial selection



Methods for detecting selection

Different types of tests analyse different patters of genetic variation:

- Within-species polymorphism can be used to detect ongoing or recent selection (Tajima's *D* would be such a test).
 ⇒ e.g., Polymorphism among maize landraces
- Polymorphism and between species divergence can also detect ongoing or recent selection (e.g. HKA test).
 ⇒ e.g., Polymorphism and divergence of maize and teosinte
- Phylogenetic comparisons between species. They are most suited for detecting historical selection.
- \Rightarrow e.g., comparisons among maize, teosinte, sorghum, rice, wheat, barley, ...

Genetic mapping of genes by analysing selection

Useful genes for plant breeding can be mapped by analysing the footprints of selection.

- · 'Natural selection mapping', 'selective sweep mapping'
- This mapping approach is often more sensitive: Identification of genes with a footprint of selection but without an obvious phenotype.

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The mutation-drift equilibrium

The mutation-drift equilibrium described by the Neutral Theory of Molecular Evolution is used as the null hypothesis of selection mapping.

It allows simple predictions as the basis of selection tests:

- Within population variation: $4N_u\mu = \theta$
- \cdot Rate of divergence per generation: μ
- Between population variation: $2t\mu$



Selection testing

- Compare the MRCA of a locus with the neutral mutation-drift expectation
- Positive selection: An allele has increased in frequency in the population \Rightarrow More recent MRCA
- Consequence: lower variation, higher LD
- Balancing selection: Different polymorphisms maintained for a long time \Rightarrow More distant MRCA
- \cdot Consequence: higher variation, lower LD



Structure of a selective sweep

Variation





Map location

Balancing selection

Local region with elevated polymorphism







Strong sweep at the Waxy locus in rice

Waxy is responsible for the 'sticky' (glutinous) rice and encodes a gene in the starch metabolism.

The genetic mutation causing the phenotype is known (gene splicing variant).

Waxy is not a domestication, but an improvement gene.





Genome-wide analysis of selection in maize

Approach: Resequencing of teosinte, landraces and improved lines:

- 35 improved maize lines
- 21 traditional landraces from Latin America
- 14 teosinte Zea mays ssp. parviglumis
- 2 teosinte Zea mays ssp. mexicana
- 1 related species *Tripsacum dactyloides* var *meridionale*

A total of 21 million SNPs were discovered!

Hufford et al., Nature Genetics (2012)

Origin of the landraces





Summary statistics of diversity

Statistic	parviglumis	landrace	improved
π	0.0059	0.0049	0.0048
π_{genic}	0.0083	0.0072	0.0071
Tajima's D	0.0412	-0.0716	-0.2132
Tajima's D _{genic}	0.4475	0.4543	0.4129
ρ	0.0088	0.0022	0.0016
$ ho_{ m genic}$	0.0139	0.0040	0.0024

83% of teosinte diversity is retained in cultivars



The XP-CLR tests measures genetic differentiation between two groups caused by selection.

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Characteristics of selected regions



About 26% of domestication and improvement features overlap.
Differences in the patters of gene expression: Domestication genes

have a larger difference than improvement genes compared to random genes. 23/29

Strength of selection

Feature	Selection coefficient (s)
Genome-wide	0.0011
Domestication	0.0150
Improvement	0.0030

Were the domestication genes discovered?

Gene Symbol	Gene Name	candidate	in candidate feature	XP-CLR feature percentile
tb1	teosinte branched1	yes*	yes*	95 th
tga1	teosinte glume architecture1	no	yes	93 rd
ra1	ramosa1	no	yes	96 th
su1	sugary1	no	yes	97 th
pbf1	prolamine-box binding factor1	no	yes	97 th
zag2	zea agamous homolog2	yes	yes	99 th
zag1	zea agamous-like1	yes	yes	94 th
bif2	barren inflorescence2	yes	yes	98 th
gt1	grassy tillers1	no	no	not in feature
ba1	barren stalk1	no	yes	99 th
bt2	brittle endosperm2	no	yes	99 th
zfl2	Zea floricaula leafy2	yes	yes	95 th
ae1	amylose extender1	no	no	not in feature

Hufford et al., 2012

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Summary

- The set of traits that differentiate a domesticated crop from its wild ancestor(s) is called domestication syndrome.
- In the different cereal crops, many domestication traits are similar, such as reduced seed shattering.
- Most known cloned domestication genes are regulatory genes with an effect on the architecture of the traits.
- Whole genome resequencing reveals novel candidate genes for domestication.

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Further reading

- Charles Darwin, On the Origin of Species, First Chapter. Download at http://www.gutenberg.org/ebooks/2009
- Doebley et al., The molecular genetics of crop domestication. Cell 127:1309 (2006)
- Hartl and Clark, Principles of Populations Genetics, 4th edition, Chapters 7.1 7.4.
- $\cdot\,$ Murphy, People Plants and Genes, Chapters 5 and 6.
- \cdot The papers cited in this lecture.
- Hufford et al. (2012) Comparative population genomics of maize domestication and improvement. Nature Genetics 44:7 (2012)

Review and discussion questions

- Summarize the key features of the mutation-drift equilibrium.
- What is the relationship between the strength of selection and the region affected by genetic hitchhiking?
- What are the features of adaptive trait genes, domestication genes, yield genes, housekeeping genes with respect to expected levels of genetic variation? At which stages of natural evolution, domestication and selection in modern breeding programs are they expected to evolve under selection, and which type of selection is acting on them?
- Why are adaptive genes identified by natural selection mapping in wild ancestors interesting for plant breeding purposes?

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References i

Hufford MB, Xu X, Van Heerwaarden J, Pyhäjärvi T, Chia JM, Cartwright RA, Elshire RJ, Glaubitz JC, Guill KE, Kaeppler SM, et al. (2012) Comparative population genomics of maize domestication and improvement. Nature Genetics 44(7):808–811