

3502-470 Plant Genetic Resources

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Outline

 \cdot Domestication syndrome

• Genes controlling domestication traits

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Charles Darwin, On the Origin of Species, Chapter 1

Sports are individuals with discontinuous mutants are important for animal and plant breeding. May not be useful in nature but selected by humans.





Figure 1: Pigeons with discontinuous muations ('sports').

Domestication syndrome

Trait	Wild Plant	Domesticated crop
Height	Tall	Short or dwarf
Growth habit	Branched and bushy	Unbranched and compact
Ripening	Asynchronous	Synchronous
Seed dormancy	Present	Absent
Seed shattering	Shattering heads	Nonshattering heads
Seed size	Small	Large
Ease of dispersal	Highly dispersible	Loss of dispersal
Threshing	Hard	Easy
Reproduction	Outbreeding	Self-fertilizing
Germination	Asynchronous	Synchronous
Hairs and/or spines	Present	Absent or reduced
Toxins	Present	Absent or reduced

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Groups of domestication traits

- \cdot Seeds: Reduced dormancy and increased germination ability and vigor
- \cdot Harvest: High yield, no seed dispersal and synchronicity
- Adaptation: Environment, cultivation and use

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Domestication syndrome in monocots and dicots



Domestication traits of barley



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Teosinte and maize inflorences

Trait	Teosinte	Maize
Kernel number	5-12 kernels	500 kernels
Seed protection	Hard casing	Naked
Central axis	Absent	Present
Attachment to axis	-	Firmly attached

Maize is completely dependent on humans:

- Ear falls to ground
- \cdot All grains mature within a short local region
- $\cdot\,$ They shade each other and prevent maturation and flowering
- \Rightarrow No reproduction!

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How many genes are responsible for differences between maize and teosinte?

There are four key traits that differentiate both:

- 1. Kernel is protected by a hard, cupulate fruitcase consisting of a glume and an invaginated rachis segment. Strongly reduced in maize.
- 2. Teosinte ears disarticulate and shatter upon maturation, whereas in maize mature kernels remain on the ear.
- 3. Each cupule fruitcase holds a single spike (kernel-bearing structure) in teosinte, but two in maize. In teosinte, the second one is present, but is aborted during development. Hence, in maize it is de-repressed.
- 4. In teosinte, cupulate fruitcases are arranged opposite in two rows. In maize they are arranged in four or more ranks (also called rows). $_{_{15/36}}$

Approach to mapping domestication genes

- \cdot Cross between maize and teosinte
- QTL mapping
- Molecular cloning of genes

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QTL analysis of domestication genes in maize



Doebley et al., 1997

a: Teosinte; b: Maize; c: Maize with mutant tb1 gene

Results of QTL analysis

- \cdot Work by John Doebley and his group
- \cdot QTLs scattered through genome
- \cdot 5 to 6 regions with a strong effect
- About 10 QTLs per trait

 \Rightarrow Complex genetic architecture with quantitative rather than Mendelian architecture

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Summary of QTL effects

QTL effects summed over nine traits (plant and inflorescence architecture) in an F_2 of maize and teosinte.



Molecular cloning of tb1

- Complex expression pattern throughout development
- \cdot It is a transcriptional regulator
- Acts as a repressor of other genes
- Mutation that differentiates teosinte and maize *tb1* alleles is in the regulatory region of the gene

tb1 expression in the shoot apex meristems



(a) Teosinte

• tb1 is not expressed at the shoot apex meristems in teosinte. Hubbard et al., 2002

tb1 expression in the female spikelets



(c) Teosinte

• tb1 is expressed in the female spikelets in both teosinte. and maize

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Regulation of transcription

tb1 is a member of the TCP family of DNA-binding transcriptional regulators (Kosugi and Ohashi 2002); it acts a repressor of transcription.

What are transcription factors?

- \cdot group of proteins that can bind to DNA in transcription factor binding sites and influence transcription of target genes
- \cdot they can activate or repress transcription (activator/repressor)

Transcription factor families

Classification by DNA-binding protein motifs:

- \cdot Helix-turn-helix proteins
- Zink-finger proteins
- Leucin zipper proteins
- \cdot Helix-loop-helix proteins

Molecular dissection of tb1 regulatory regions

- The causal mutation is located in a genomic intervall of 160 kb between two genes, *pg3* and *tb1*
- Approach: Introgression of a teosinte fragment into maize by backcrossing and fine mapping

Table 1 Traits analyzed and phenotypic effects



Clark et al., Nature Genetics (2006)

Mapping of the causal mutation to a region of 10 kb



Clark et al., Nature Genetics (2006)^{26 / 36}

Transposable elements (TE)

- Discovered by Barbara McClintock in the 1940s in Maize (Nobel prize).
- TE classes differ in structure and the mechanism of transposition.
- TEs that require reverse transcription (transcription of RNA to DNA): Retrotransposons
- TEs that use a **transposase** for insertion and excision: **DNA transposons**
- Autonomous TEs: transpose themselves
- Non-autonomous TEs: need other TEs in the vicinity to assist in transposition

Further reading: http://www.nature.com/scitable/topicpage/ transposons-the-jumping-genes-518



Further fine-scale mapping

Approach:

- Make teosinte introgressions isogenic
- Evaluate in field trials
- Estimate additive effects with mixed linear model

Results:

- \cdot Two independent components affect phenotype
- Distal and proximal part of 10 kb control region

Studer et al., Nature Genetics (2011)

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Fine-scale mapping of tb1



Studer et al., Nature Genetics (2011)^{30 / 36}



Studer et al., Nature Genetics (2011)

Conclusion of fine-scale mapping

- $\cdot\,$ Both proximal and distal regions contribute to phenotype
- Strongest effect seen by the insertion of a transposable element, *Hopscotch* in maize
- Domesticated phenotype caused by transposable element!
- $\cdot\,$ Transposon insertion predates domestication by 10,000 years
- Selection of *tb1* on standing genetic variation!



Summary

- Despite clear discontinous phenotypic differences between ancestral and domesticated plants, the genetic architecture is quantitative and complex
- teosinte-branched 1 is one of the best characterized domestication genes
- Many domestication genes are transcriptional regulators
- The causal 'domestication' mutation regulates the expression of *tb*1
- The main effect of the domesticated allele results from a transposon insertion

Further reading

- Doebley (2004), The genetics of maize evolution.
- Clark et al., A distant upstream enhancer at the maize domestication gene *tb1* has pleiotropic effects on plant and inflorescent architecture. Nature Genetics (2006)
- Studer et al., Identification of a functional transposon insertion in the maize domestication gene *tb1*. Nature Genetics (2012)

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Review questions

- What is the domestication syndrome and how is it characterized? Are all crop species expected to have all characteristics of the domestication syndrome?
- What are the characteristics of 'sports' described by Darwin in the first chapter of the 'Origin of Species'? Why are they relevant for domestication and plant breeding? What would be the fate of these sports in naturally evolving (i.e., without human intervention) populations?
- What are the common and what are the different features of the domestication syndromes of barley, rye and maize?
- How does the *tb1* of maize change the plant architecture?
- How can information about the genetic basis of domestication genes used for breeding of maize or other crops?

References i

Doebley J (2004) The genetics of maize evolution. Annual Review of Genetics 38(1):37–59, DOI 10.1146/annurev.genet.38.072902.092425, URL https:

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