

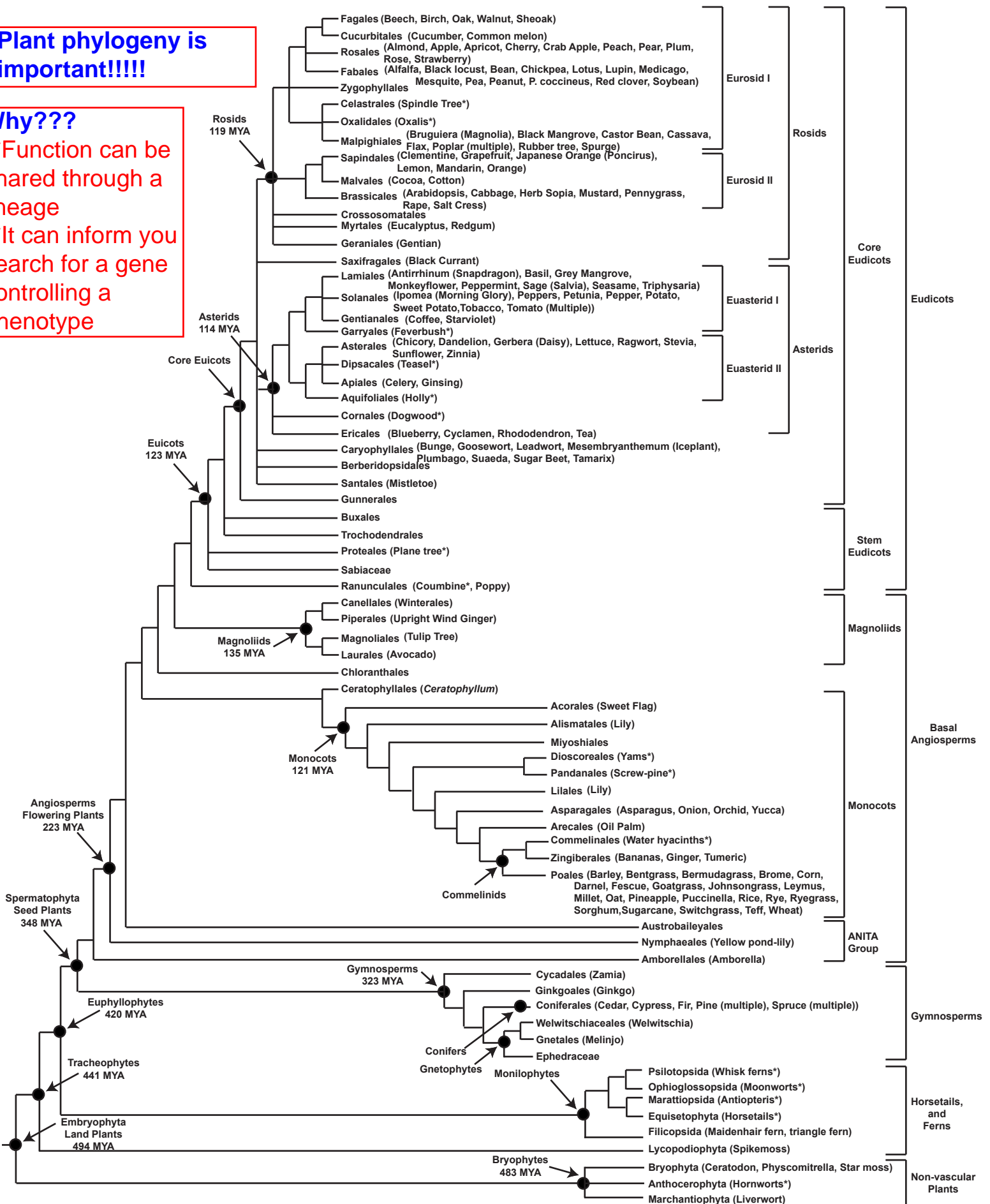
# Phylogenetic Relationships and Divergence Times of Land Plants Orders

Plant phylogeny is important!!!!

Why???

\*\*Function can be shared through a lineage

\*\*It can inform you search for a gene controlling a phenotype

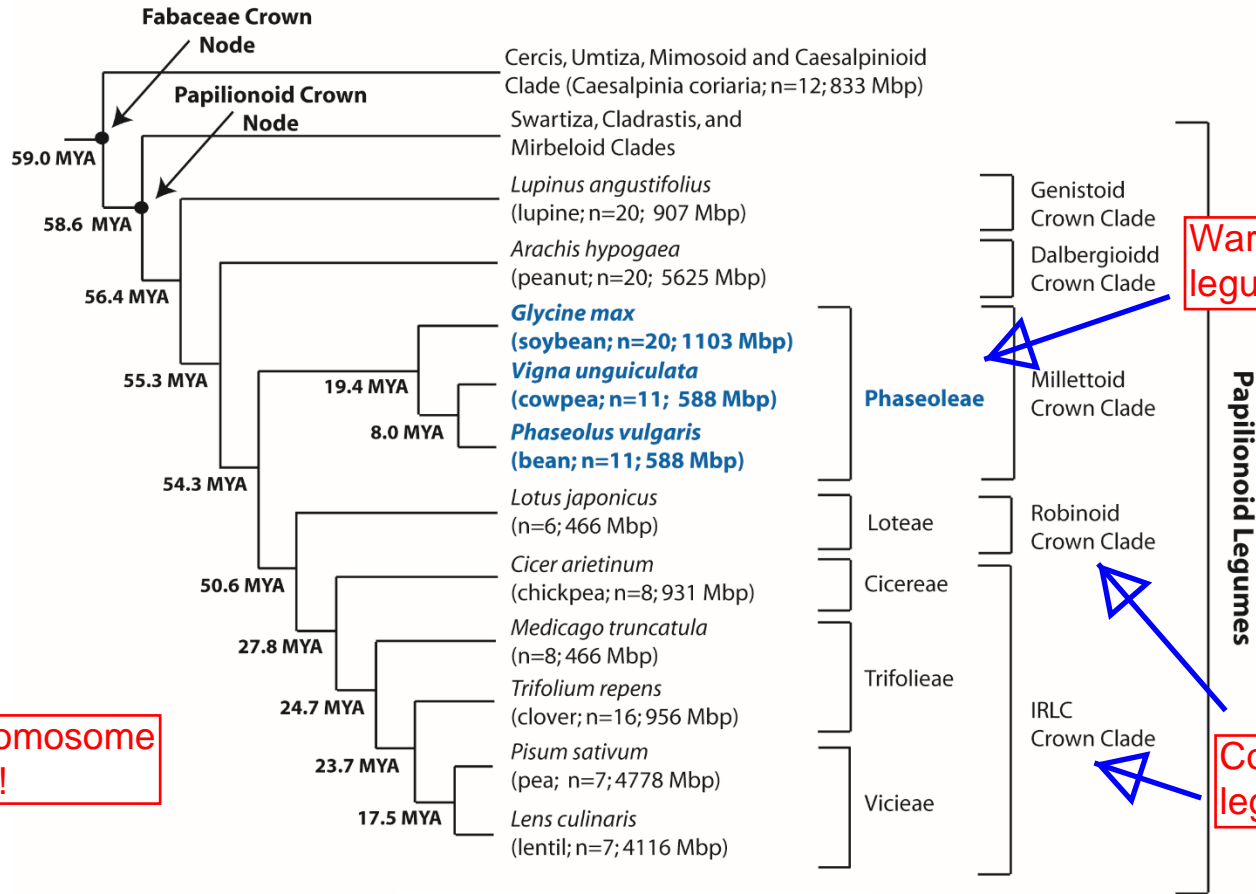


The dating of the orders in the eucicots was based on Magallón et al., (2015; New Phytologist 207, 437-453). All other datings were based on the results (mean of range) for the monophyletic model presented in Table 3 of Morris et al., (2018 Proceedings of the National Academy of Sciences, 115, E2274-E2283).

# Deep Phylogeny

**\*\*Important when choosing a species to search for shared functional gene**

## Phylogeny of Fabaceae with Legume Focus



**Note chromosome number!!!**

**Warm-season legumes**

**Cool-season legumes**

# Know Important Statistics for Your Species

## Major crops of the world

Crop class	2012 Mha harvested*	% All crops
Cereals	703	64.4
Oilcrops	256	23.4
Pulses	78	7.1
Roots and Tubers	55	5.1

Rank	Crop	2012 Harvested acres
1	Wheat	216,638,762
2	Maize	176,991,927
3	Rice, paddy	163,463,010
4	Soybeans	106,625,241
5	Barley	49,310,546
6	Sorghum	37,851,779
7	Seed cotton	34,368,366
8	Rapeseed	34,257,051
9	Millet	31,230,341
10	Beans, dry	28,780,377
11	Sugar cane	25,762,157
12	Sunflower seed	25,011,871
13	Groundnuts, with shell	24,625,099
14	Cassava	19,990,556
15	Potatoes	19,321,198
16	Oil, palm fruit	16,413,436
17	Chick peas	12,144,639
18	Coconuts	12,002,505
19	Cow peas, dry	10,688,653
20	Olives	9,984,919
21	Oats	9,627,546
22	Sesame seed	8,051,612
23	Sweet potatoes	8,050,003
24	Peas, dry	6,326,999
25	Pulses	5,903,158

## Calories

		2009
Rank	Items	kcal/capita/day
1	Rice (Milled Equivalent)	536
2	Wheat	532
3	Sugar (Raw Equivalent)	194
4	Maize	141
5	Soyabean Oil	80
6	Vegetables, Other	67
7	Potatoes	61
8	Palm Oil	53
9	Cassava	37
10	Rape and Mustard Oil	35
11	Sunflower seed Oil	33
12	Pulses, Other	32
13	Sorghum	32
14	Beer	31
15	Fruits, Other	28
16	Millet	27
17	Beverages, Alcoholic	24
18	Beans	22
19	Sweet Potatoes	22
20	Sweeteners, Other	22
21	Groundnuts (Shelled Eq)	21
22	Bananas	20
23	Groundnut Oil	16
24	Soyabeans	15
25	Nuts	14

## Protein Source

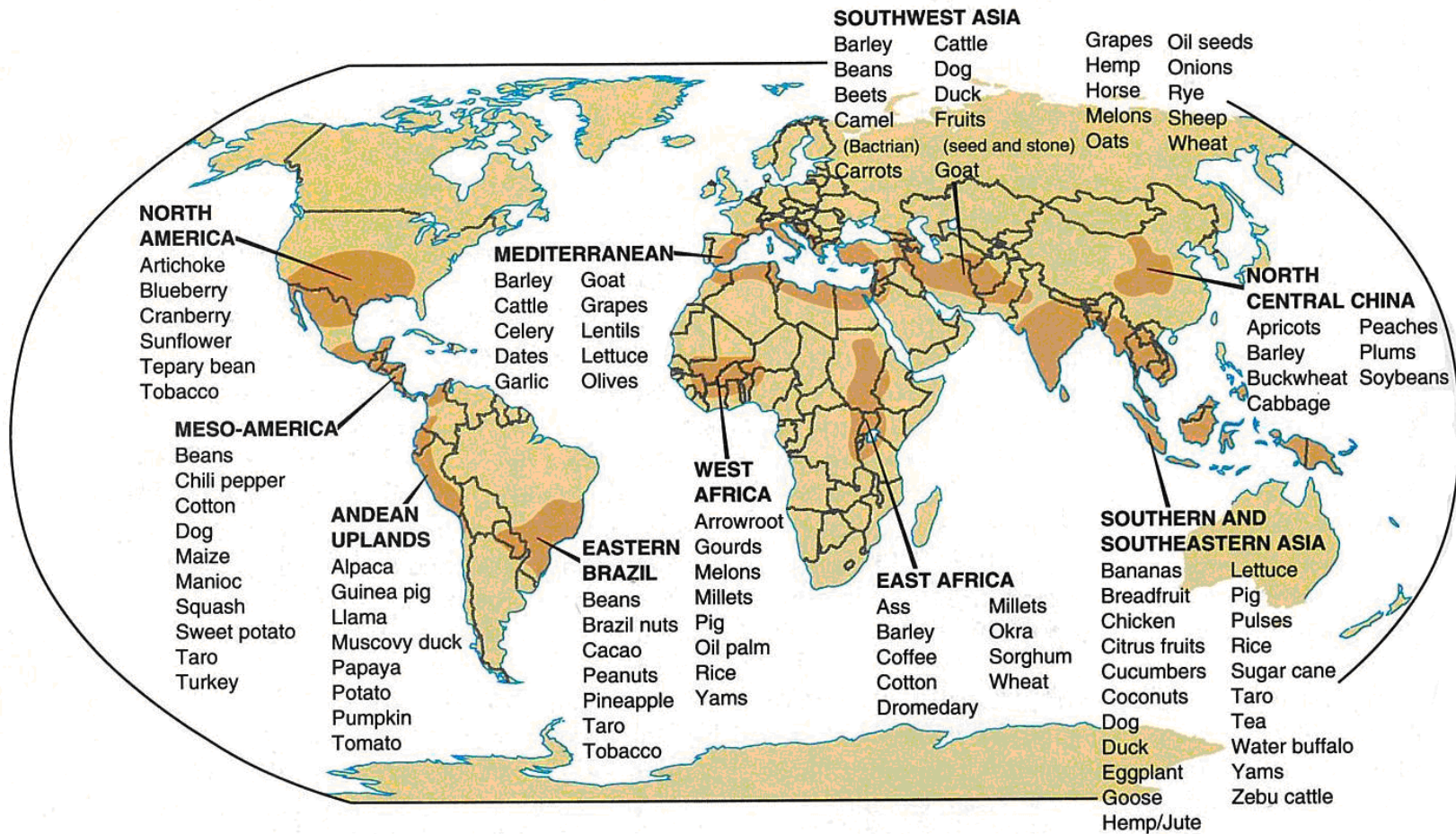
<b>Rank</b>	<b>Crop</b>	<b>2009 g protein/capita/day</b>
1	Wheat	16.2
2	Rice (Milled Equivalent)	10.1
3	Vegetables, Other	3.6
4	Maize	3.4
5	Pulses, Other	2.0
6	Beans	1.4
7	Potatoes	1.4
8	Soyabeans	1.4
9	Sorghum	1.0
10	Groundnuts (Shelled Eq)	0.9
11	Millet	0.7
12	Peas	0.5
13	Tomatoes	0.5
14	Nuts	0.4
15	Onions	0.4
16	Bananas	0.3
17	Beer	0.3
18	Fruits, Other	0.3
19	Barley	0.2
20	Cassava	0.2
21	Cereals, Other	0.2
22	Coffee	0.2
23	Oranges, Mandarines	0.2
24	Rye	0.2
25	Spices, Other	0.2

## Major Crops in the United States

Production Value at Farm Gate: 2009-2018 Change

All values are times \$1,000!!!

Rank 2018		Value 2018 (\$)	Rank 2009	Value 2009 (\$)	Order	Group
1	Corn for Grain	51,581,090	1	48,588,665	Poales	Monocot
2	Soybeans for Beans	39,133,978	2	31,760,452	Fabales	Eurosid I
3	Hay, All (Alfalfa+Others)	17,048,184	3	14,990,083	Fabales	Eurosid I
4	Wheat, All	9,699,073	4	10,626,176	Poales	Monocot
5	Cotton, All+Cottonseed	7,083,480	5	4,401,710	Malvales	Eurosid II
6	Grapes	6,507,849	7	3,171,814	Vitales	Rosid incertae sedis
7	Almonds (CA)	5,603,950	14	1,780,350	Rosales	Eurosid I
8	Potatoes	3,853,027	6	3,452,276	Solanales	Euasterid I
9	Apples, Comm'l	3,601,447	10	2,222,759	Rosales	Eurosid I
10	Rice	2,751,514	8	3,145,521	Poales	Monocot
11	Lettuce, All	2,706,342	11	2,175,431	Asterales	Euasterid II
12	Strawberries	2,670,523	12	2,123,735	Rosales	Eurosid I
13	Oranges	1,943,678	13	1,950,452	Sapindales	Eurosid II
14	Tomatoes, All	1,856,280	9	2,532,853	Solanales	Euasterid I
15	Sugarbeet*	1,456,165			Caryophyllales	
16	Beans, All	1,341,582	17	1,209,064	Fabales	Eurosid I
17	Mushrooms	1,233,582	19	957,028	Fungi	Fungus
18	Sorghum	1,212,237	16	1,242,196	Poales	Monocot
19	Peanuts	1,155,709	22	835,172	Fabales	Eurosid I
20	Tobacco	1,093,918	15	1,498,629	Solanales	Euasterid I
21	Sugarcane*	1,025,524			Poales	Monocot
22	Pistachios	1,014,507	23	787,440	Sapindales	Eurosid II
23	Cherries*	958,520			Rosales	Eurosid I
24	Corn, Sweet, All	858,862	18	1,171,396	Poales	Monocot
25	Blueberries*	833,469			Ericales	
26	Onions	817,496	21	843,570	Asparagales	Monocot
27	Lemon*	763,446			Sapindales	Eurosid II
28	Broccoli, All	738,527	24	741,900	Brassicales	Eurosid II
29	Barley	693,058	20	917,500	Poales	Monocot
30	Watermelon*	656,655			Cucurbitales	Eurosid I
31	Peaches	599,862	25	595,103	Rosales	Eurosid I



**Figure 7-1.** This map shows the origins of the world's food crops and domesticated animals. These plants and animals have been so widely redistributed, however, that today's leading producers of many of these are not the same as the areas in which they were first domesticated.

from: <http://earthday.net>

## What is domestication?

**Domestication:** selecting plants and animals for human usage; domestication was a major event the transition of humans from a nomadic species to a species that resides a defined location

## Uses of domesticated species

- Abundant food source
- Fiber for construction

## Functional features

- Adapted to agricultural practices
- Ease harvest
- Taste great (and so good for you)
- Pleasing to the eye
- Storage

1840-1850

Corn clubs

Make crosses

Share crosses

Flint

Dent

Stiff stalk

Non-stalk

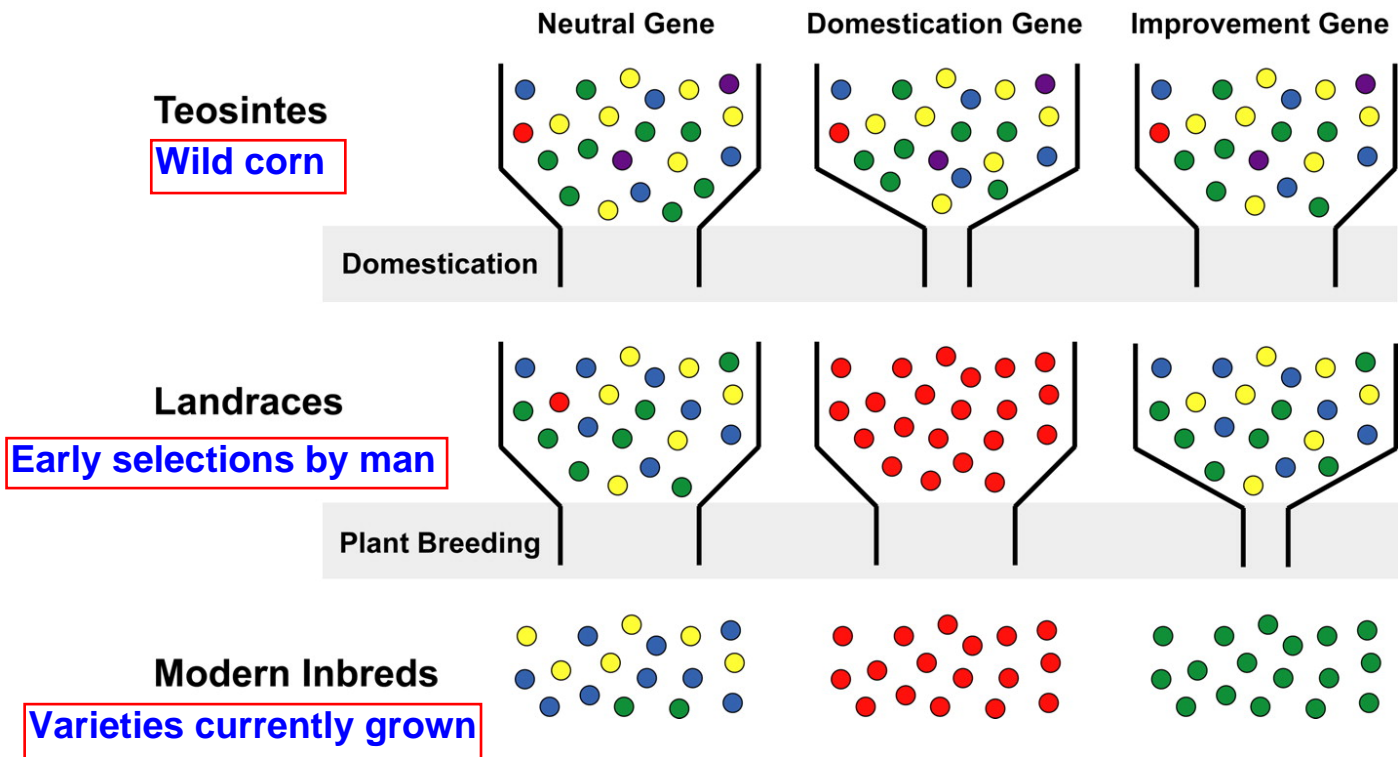
## What is crop improvement?

**Improvement:** the development selection of traits that enhance the usage and functional features of a crop; often associated with modern plant breeding although initially improvement was applied to already domesticated germplasm



**Transitions from WILD to MODERN varieties**  
\*\*What genes change allele frequency????

## The Effect of Domestication on Diversity



From: **Yamasaki et al. (2005)** A Large-Scale Screen for Artificial Selection in Maize Identifies Candidate Agronomic Loci for Domestication and Crop Improvement . *Plant Cell* 17: 2859.

**Neutral genes:** the frequency of the alleles of these genes is affected to only a small degree by domestication and improvement

**Domestication genes:** the frequency of one allele domestication genes increases greatly during the domestication process and remains the same through the improvement process

**Improvement genes:** the frequency of alleles of improvement genes remains the same during domestication but one allele moves to a high frequency during the improvement process

## Major Changes Following Domestication

Not all traits are found in all domesticated species

- **Size**
  - Larger plant size (biomass)
- **Yield**
  - Larger size of harvestable unit
  - Greater harvest index
  - Increased ratio of harvestable unit weight to total plant biomass at harvest
- **Plant stature**
  - Reduced plant height
  - Determinate vs. indeterminate
- **Phenology**
  - Reduced days to flowering
  - Reduced days to maturity
- **Other**
  - Loss of dormancy requirement
  - Loss of seed dispersal mechanism
  - Loss of photoperiod sensitivity

**Examples of Domestication Traits** [from: Doebley et al. (2006) The Molecular Genetics of Crop Domestication. Cell 127: 1309)

**Maize:** The wild plant is highly branched with the kernel encased. The maize plant has a single stalk and naked kernels. The branching/single stalk trait is controlled by the *Tb1* gene, while the *Tga1* gene responsible for the presence/absence of the casing. *Tga1* is a member of the **SBP family of transcription factors**.

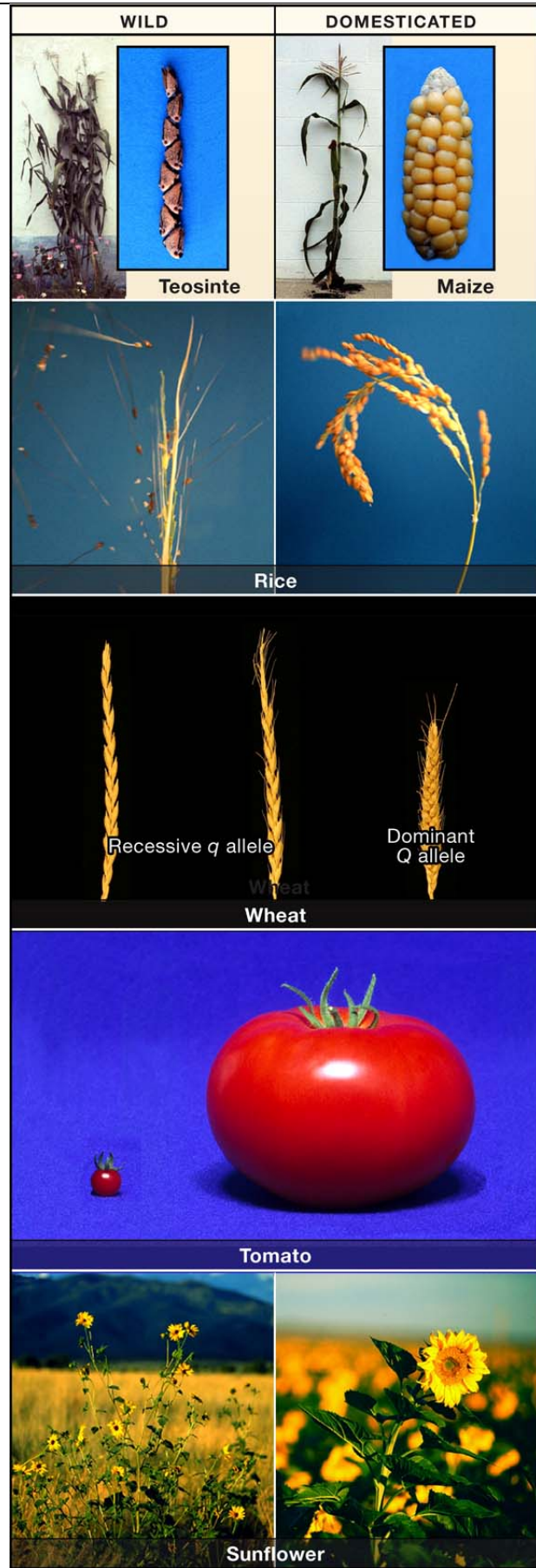
**Rice:** The wild rice panicle shatters and the kernel is dispersed while the domesticated rice kernel stays within the panicle enabling ease of harvest. The difference between the phenotypes is the result of the *Sh4* gene, a transcriptional regulator gene from the **Myb family of transcription factors**.

**Wheat:** The wild wheat has a slender, fragile spike while the domesticated wheat has a condensed, tough spike. The difference is the result of different alleles at the *Q* gene. This gene encodes a member of the **AP2 transcription factory family**.

**Tomato:** The wild tomato has a very small fruit while the domesticated fruit is large. This difference is controlled by the *fw2.2* gene. Cysteine-rich protein that **negatively regulates cell division**.

Every QTL has a functional gene in its interval  
 \*\**fw2.2* original defined as a QTL  
 \*\*first QTL cloned in plants

**Sunflower:** The difference between wild and domesticated sunflower is the presence of many small heads in the wild and a single head in the cultivated germplasm.



**Barbara McClintock**\*\*Cell division in *Neurospora*

\*\*Crossing over involves exchange of chromosomal material

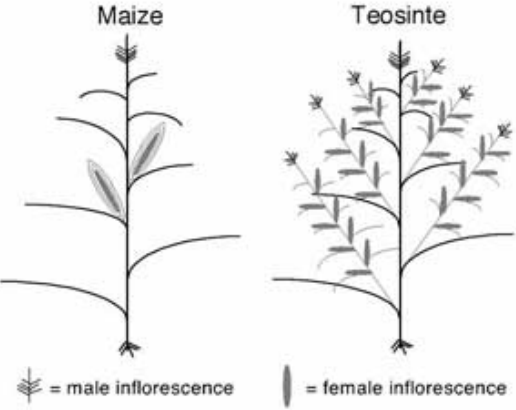
\*\*Transposable element

**"Feeling for your organism"****Example from Common Bean**Koinange et al (1996) *Crop Science* 36:1037

General attribute	Trait	Wild: G12873	Domesticated: 'Midas'
Seed dispersal	Pod suture fibers ( <i>St</i> )	Present	Absent
	Pod wall fibers ( <i>St?</i> )	Present	Absent
Seed dormancy	Germination (DO)	58%	100%
Growth habit	Determinacy ( <i>fin</i> )	Indeterminate	Determinate
	Twining ( <i>Tor</i> )	Twining	Non-twining
	Number of nodes on the main stem (NM)	23	8
	Internode length (L5)	1.9 cm	2.6 cm
	Number of pods (NP)	29	17
Gigantism	Pod length (PL)	5.7 cm	9.6 cm
	100-seed weight (SW)	3.5 g	19.5 g
Phenology	Number of days to flowering (DF)	69	46
	Number of days to maturity (DM)	107	80
Photoperiod sensitivity	Number of days to flowering under 16 h days (PD)	44	35
Harvest index	Seed yield/total above-ground biomass (HI)	42%	62%
Seed pigmentation	Presence vs. absence ( <i>P</i> )	Present (agouti)	Absent (white)

# Maize Domestication Changes

From: <http://teosinte.wisc.edu/morphology.html>

Image of maize and teosinte difference	Quotes from above WWW site
 <p data-bbox="414 825 511 856"><b>Figure 1</b></p> <div data-bbox="272 968 695 1066" style="border: 1px solid red; padding: 5px; color: blue; font-weight: bold;">       Branching control gene        **<i>Tb1</i> </div>	<p data-bbox="764 394 1430 552">“<b>Plant Architecture:</b> Teosinte plants have main stalks that typically bear an elongate lateral branch at most nodes (Figure 1). The lateral branches and the main stalk are both composed of a series of nodes and elongated (15 or more cm long) internodes with a leaf attached at each node.</p> <p data-bbox="764 556 1430 1192">The number of internodes (or leaves) in each lateral branch is roughly equivalent to the number in the main stalk above the point of attachment of the branch. Thus, a branch attached to the third node below the main tassel will be composed of about three internodes, while one attached at the sixth node below the tassel will have about six internodes. The leaves along the lateral branches are fully formed and composed of two parts -- a sheath that clasps around the stem and a blade that extends away from the plant. The leaves on the branches are arranged in an alternate phyllotaxy, i.e. each leaf is borne on the opposite side of the stem relative to the leaves at the nodes above and below. Both the main stem and the primary lateral branches of the teosinte plant are tipped by male inflorescences (tassels) while the slender female inflorescences (ears) of teosinte are borne on secondary branches in the axils of the leaves along the primary branches. Each of these female inflorescences is surrounded by a single, bladeless leaf or husk. The ears occur in clusters of 1 to 5 (or more) at each node along the branch.</p> <p data-bbox="764 1197 1430 1871">The architecture of the lateral branches of the maize plant is strikingly different from that of teosinte (Fig. 1). Maize typically produces branches at only two or three of the nodes along the main stem. Axillary buds are present at some of the other nodes but they are arrested early in development. Each of the branches that are produced is composed of nodes and short internodes, averaging about 1 cm in length. Unlike teosinte, the number of internodes in the lateral branch is greater than the number in the main stalk above the point of attachment of the branch. For maize line W22, a branch attached at the fifth node below the main tassel will be composed of about 12 internodes and have 12 husk leaves. The leaves (husks) along the lateral branch are composed largely of sheath with only a small (if any) blade attached to it. The husks are arranged in a spiral phyllotaxy along the branch, rather than the alternate phyllotaxy for leaves on the main stem of the plant. Secondary branches are normally absent (aborted). Finally, the lateral branch is terminated by a female inflorescence or ear, which is tightly enclosed within the spirally arranged husks because of the failure of the internodes of the branch to fully elongate.”</p>

## Seed Casing

\*\**Tga* gene

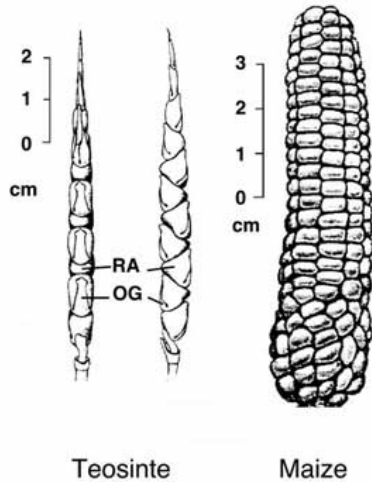


Figure 2

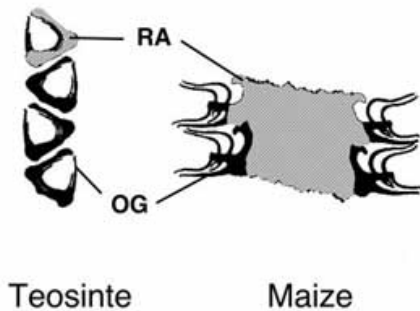


Figure 3

**“Inflorescence Architecture:** The most dramatic differences between maize and teosinte involve the architecture of their female inflorescences (Figs. 2 and 3). The teosinte ear is composed of 5 to 10 (or more) distichously (in two ranks) arranged cupulate fruitcases. The cupule of the cupulate fruitcase is formed from the invaginated rachis internode (RA). The cupule contains a single sessile spikelet that is oriented parallel to the axis of the rachis. The outer glume (OG) of this sessile spikelet seals the opening of the cupule, thus obscuring the kernel from view. Both the rachis internode and its outer glume are highly indurated in teosinte. The cupulate fruitcases are separated from one another by abscission layers, thus enabling the fruitcases to separate (disarticulate) at maturity for dispersal.

The cob (rachis) of the maize ear, like that of its teosinte counterpart, is composed of invaginated internodes or cupules (Figs. 2 and 3). Maize cupules are arranged polystichously (in four or more ranks) around the circumference of the ear with usually 100 or more cupules in a single ear (Fig. 2). Unlike teosinte, the cupules of maize are shallow, often collapsed, and they do not envelop the kernels (Figs. 2 and 3). Maize cupules may be indurate, but the outer glumes are softer than the highly indurated glumes of the teosinte ear. In contrast to teosinte, there are two spikelets associated with each cupule, one pedicellate and the other sessile. Thus, an ear with four ranks of cupules will have eight rows of kernels (Fig. 3). The female spikelets of maize also differ from those of teosinte in that they are oriented perpendicular and not parallel to the axis of the ear. Finally, maize ears lack abscission layers as found in teosinte, so the ear remains intact at maturity.”

**Wild vs. Domesticated Millet**

**\*\*Highly branched**

**\*\*Less seeds**

**WILD MILLET**



**DOMESTICATED MILLET**



# Wheat domestication

[from Tanno and Willcox (2006) Science 311:1886]

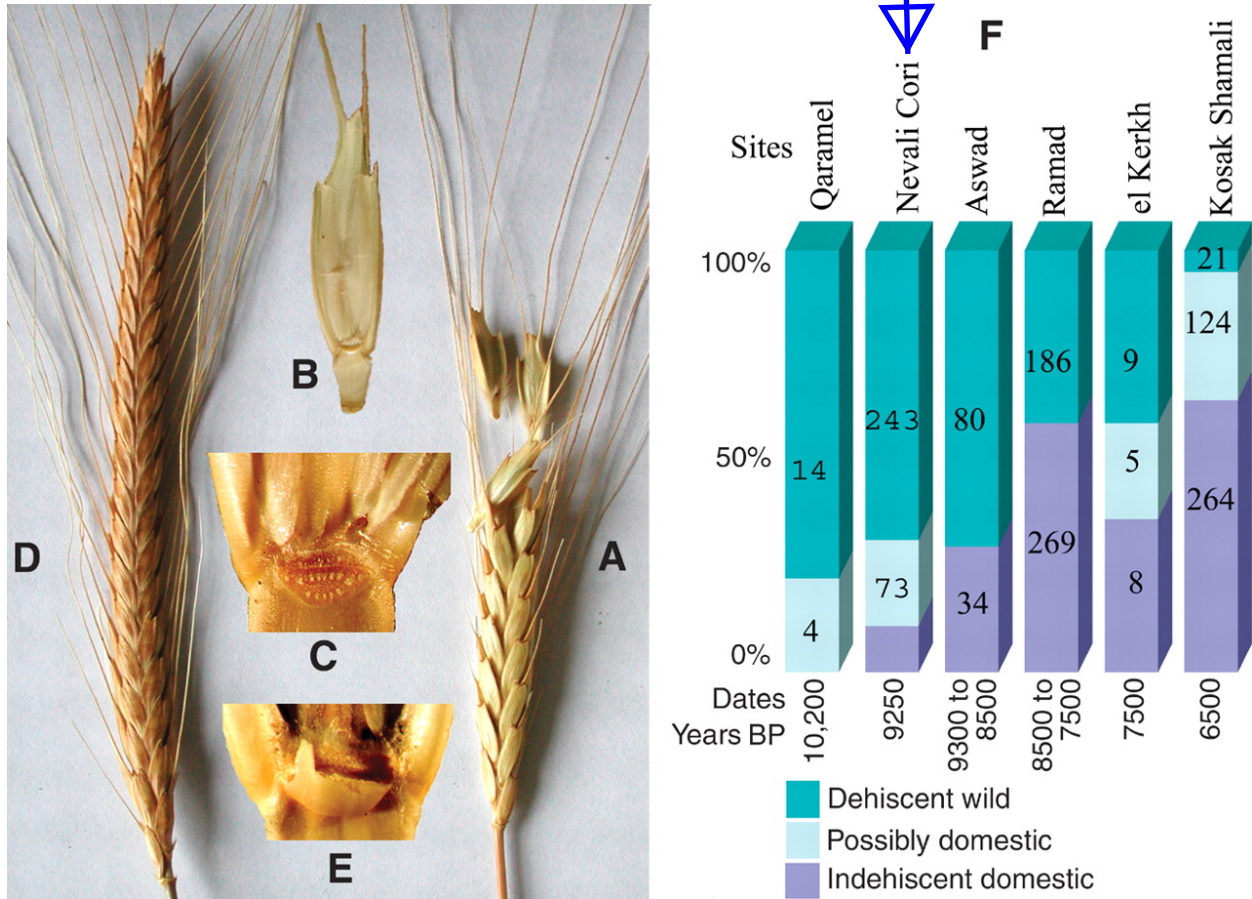


Fig. 1. Modern examples of dehiscent wild einkorn wheat ear (A) and spikelet (B). Detail of spikelet with smooth wild abscission scar (C), indehiscent domestic ear (D), and detail of spikelet with jagged break (E) are shown. The bar chart (F) gives relative frequencies of subfossil finds with the absolute figures. Records from Aswad and Ramad (6) are of barley; the other four sites are of wheat. For full data of both studies, see table S1.



General WWW site:

<https://www.thoughtco.com/plant-domestication-table-dates-places-170638>

Plant	Where Domesticated	Date
Fig trees	Near East	9000 BC
Emmer wheat	Near East	9000 BC
Foxtail Millet	East Asia	9000 BC
Flax	Near East	9000 BC
Peas	Near East	9000 BC
Einkorn wheat	Near East	8500 BC
Barley	Near East	8500 BC
Chickpea	Anatolia	8500 BC
Bottle gourd	Asia	8000 BC
Bottle gourd	Central America	8000 BC
Rice	Asia	8000 BC
Potatoes	Andes Mountains	8000 BC
Beans	South America	8000 BC
Squash (Cucurbita pepo)	Central America	8000 BC
Maize	Central America	7000 BC
Water Chestnut	Asia	7000 BC
Rye	Southwest Asia	6600 BC
Broomcorn millet	East Asia	6000 BC
Bread wheat	Near East	6000 BC
Manioc/Cassava	South America	6000 BC
Chenopodium	South America	5500 BC
Date Palm	Southwest Asia	5000 BC
Avocado	Central America	5000 BC
Grapevine	Southwest Asia	5000 BC
Cotton	Southwest Asia	5000 BC
Bananas	Island Southeast Asia	5000 BC
Beans	Central America	5000 BC
Opium Poppy	Europe	5000 BC
Chili peppers	South America	4000 BC
Amaranth	Central America	4000 BC
Watermelon	Near East	4000 BC
Olives	Near East	4000 BC
Cotton	Peru	4000 BC
Apples	Central Asia	3500 BC
Pomegranate	Iran	3500 BC
Garlic	Central Asia	3500 BC
Hemp	East Asia	3500 BC
Cotton	Mesoamerica	3000 BC
Soybean	East Asia	3000 BC
Azuki Bean	East Asia	3000 BC
Coca	South America	3000 BC
Squash (Cucurbita pepo o.)	North America	3000 BC
Sunflower	Central America	2600 BC
Rice	India	2500 BC
Sweet Potato	Peru	2500 BC
Pearl millet	Africa	2500 BC
Sesame	Indian subcontinent	2500 BC

### Crop Domestication

**\*\*An on-going process as man settled into communities**

Sorghum	Africa	2000 BC
Sunflower	North America	2000 BC
Bottle gourd	Africa	2000 BC
Saffron	Mediterranean	1900 BC
Chenopodium	China	1900 BC
Chenopodium	North America	1800 BC
Chocolate	Mesoamerica	1600 BC
Coconut	Southeast Asia	1500 BC
Rice	Africa	1500 BC
Tobacco	South America	1000 BC
Eggplant	Asia	1st century BC
Edamame	China	13th century AD
Vanilla	Central America	14th century AD

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# KEYS TERMS

**Homolog:** genes with a shared ancestry

**Orthologs:** genes related by descent in a taxonomy

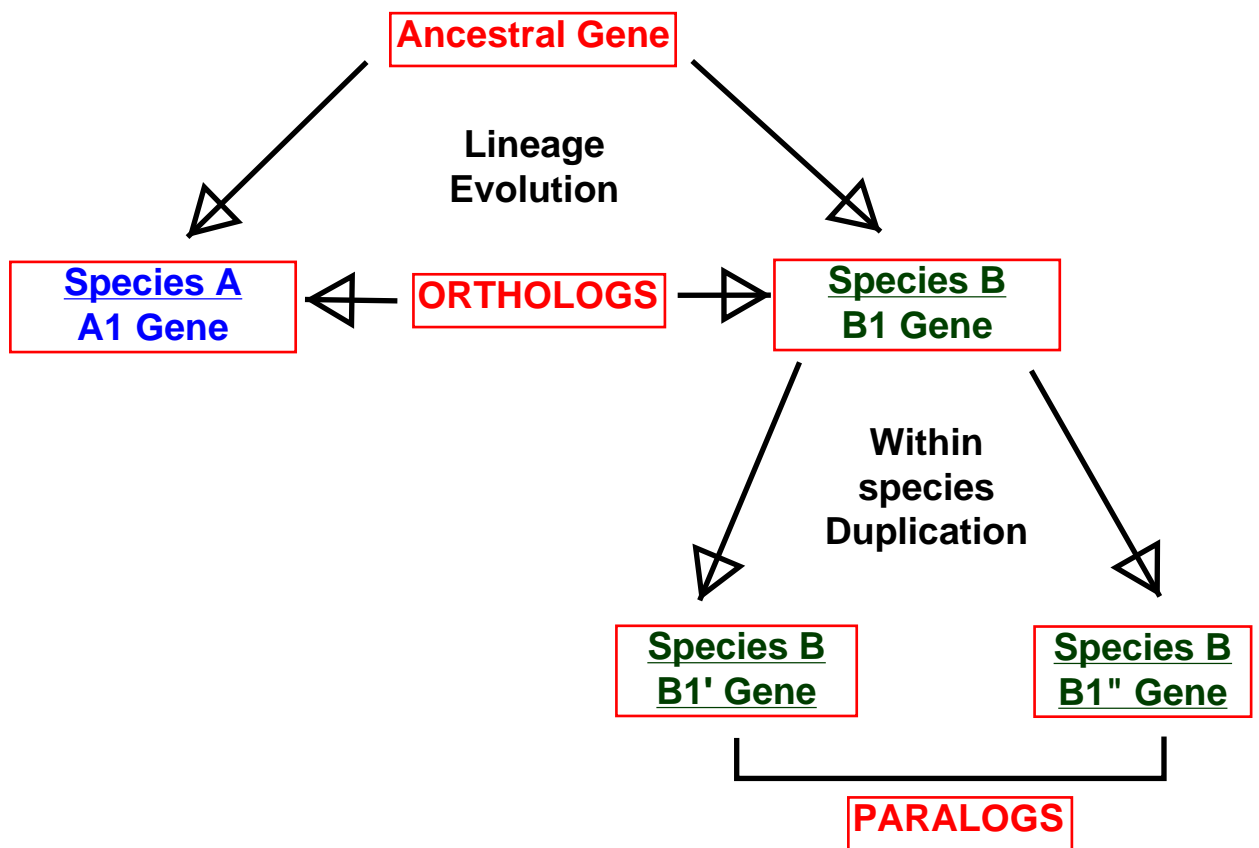
**\*\*TFL1 indeterminacy gene**

**\*\*\*TFL1, SP, Dt1, Fin**

**Paralogs:** genes related by duplication in a species

**\*\*NLR genes in plants**

**\*\*\*NB-ARC, leucine-rich repeat gene families in all plant species**



## The Appearance of Domestication Traits

- An evolution perspective

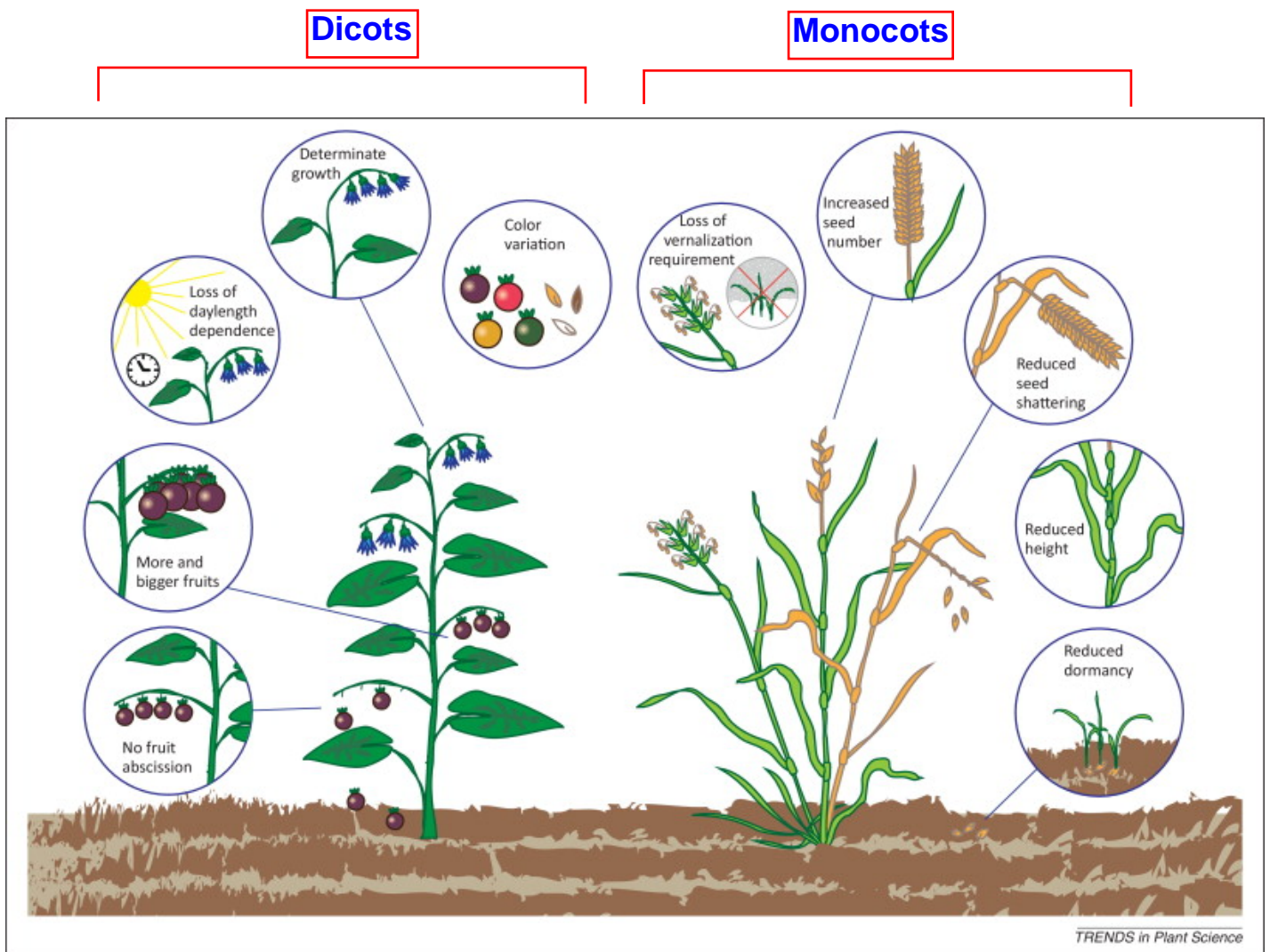
**See:** Arendt and Reznick (2008) Convergence and parallelism reconsidered: what have we learned about the genetics of adaptation? Trends in Ecology & Evolution 23:26.

**See for alternate opinion:** Lenser and Theißen (2013) Molecular mechanisms involved in convergent crop domestication. Trends in Plant Science 18:704.

### Terms to know

Sometimes referred to as  
**\*\*Molecular Convergence**

- **Convergence**
  - Appearance of the same phenotypic trait in different species by mutation in the **same gene**
    - Presence/absence of color in seed or fruit ( **$\beta$ -Helix-Loop-Helix factor**)
    - Lighter/dark coat color in animals (**melanocortin-1 receptor**)
- **Parallelism**
  - The appearance of the same phenotypic trait within a species lineage by **different** genetic mechanisms
    - Absence of seed color in beans ( **$\beta$ -HLH factor**) and soybean (**chalcone synthase anti-sense RNA**)



## Convergence in figure as defined by Lenser and Theißen (2013)

**Figure 1. Convergent domestication.** Convergent phenotypic changes are frequently observed in many different crops because systematic human cultivation often brings about similar demands. Attempts to maximize yield cause selective pressure for an **increase in size and number of edible plant parts** on the one hand and for a **decrease in natural seed and fruit dispersal mechanisms** to reduce yield loss on the other hand. Shifts in cultivation area often require changes in **day length dependence** or in the **vernalization requirement** and a **reduction in seed dormancy** is needed for synchronous germination. Small plants with a **determinate growth habit** are often selected because they are more robust, have a better yield to overall biomass ratio, and are better suited to mechanical harvesting methods. Finally, satisfying esthetic preferences often drives convergent adaptations, a prominent example being **changes in color**. Stylized examples of the major angiosperm plant lineages from which current crops originated are shown (eudicot, left; monocot, right) featuring traits of typical wild species. Characters that convergently evolved in various domesticated crops are depicted in circles.

**THESE ARE ALL DOMESTICATION TRAITS!!!**  
**\*\*All needed for the species to be a crop useful to humans!!!**

## Real-World Questions of interest for Common Crop Domestication Trait

- Was a **single gene** altered in all species OR
- Were **different genes** in a related/different pathway responsible?
  - Answer is directly related to phenotypic redundancy in a species/lineage

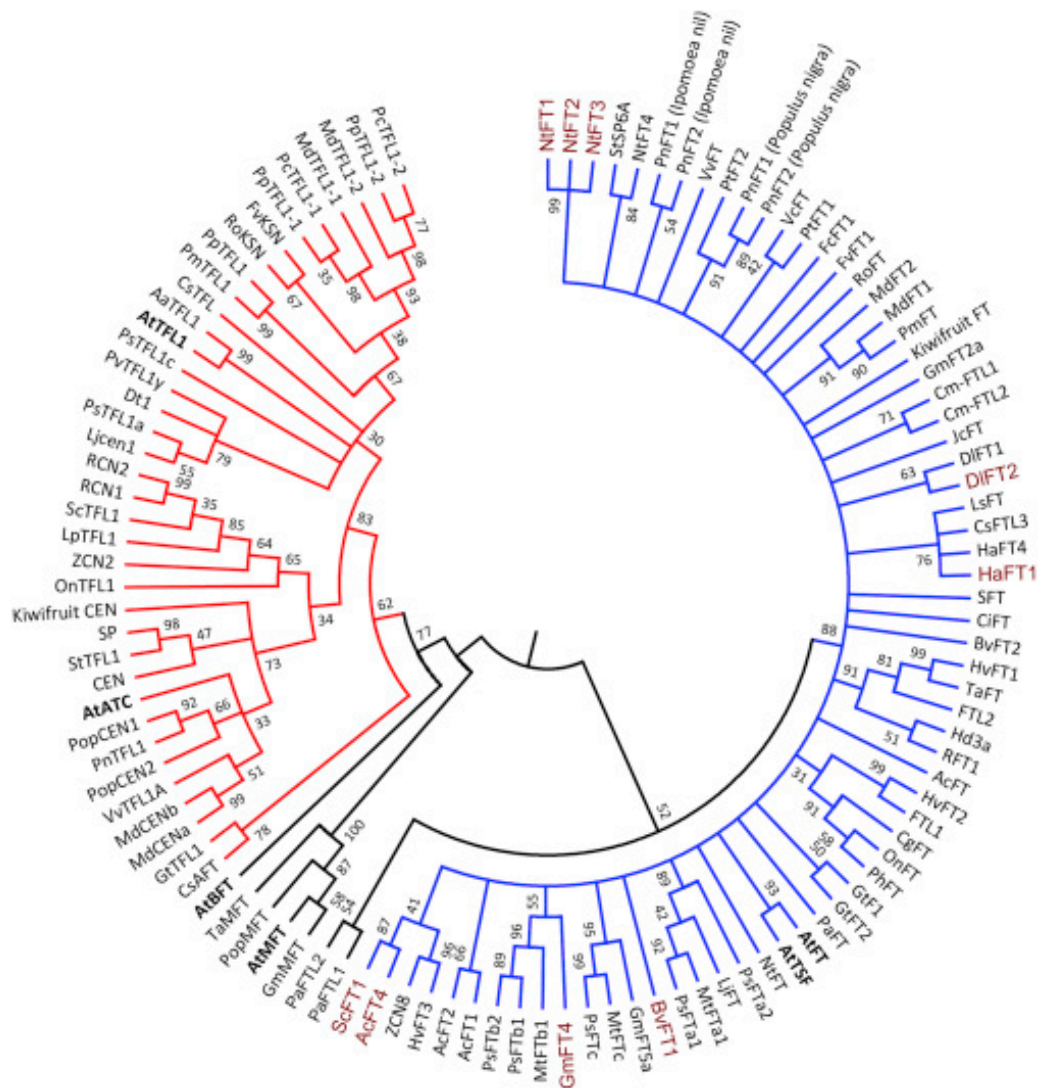
### Example of a domestication trait widely control by a single gene

### Growth Habit: Determinacy Convergent Evolution Example

#### ***TFL1* gene**

- Originally described in Arabidopsis
- Induced by the flowering pathway gene *CO*
- *TFL1* functions by repressing downstream flowering pathway genes
- Also controls determinate vs. indeterminate growth habit
  - Indeterminate is dominant
  - *TFL1* negatively regulates the onset of flowering in terminal buds
  - Mutants orthologs of *TFL1* have a determinate growth habit
    - Arabidopsis: *TFL1* (terminal flower) \*\*\*\*
    - Tomato: *SP* (self-pruning) \*\*\*\*
    - Soybean: *Dt1* (determinacy) \*\*\*\*
    - Common bean: *Fin* (finitus; finished in Latin) \*\*\*\*
      - Example of **convergent evolution between species**
  - Multiple mutations of *TFL1* also found within a species
    - Common bean
      - Eight unique **alleles** control determinacy
    - Soybean
      - Four unique **genes** control determinacy
        - Example of **parallel evolution within species**

**Exception!!!**



Wickland and Hanzawa (2015) The *FLOWERING LOCUS T/TERMINAL FLOWER 1* Gene Family: Functional Evolution and Molecular Mechanisms. *Molecular Plant* 8: 983.

- **TFL1** is **homologous** to the universal flowering regulator **FT**.
- Both share a role in flowering.
  - **FT** is a convergence point for multiple cues that activate flowering.
  - **TFL1** is critical for determinate growth habit.

**FT and TFL1 are homologs**  
**\*\*FT functions by suppressing TFL1 role in flowering**  
**\*\*Example of homologous genes evolving different functions in the same pathway**





- Brassica: *BrFLC1*
  - MADS-box transcription factor
  - Interacts with the vernalization pathway
    - Mutant alleles delay flowering
- Soybean: *E1*
  - Suppressor of *FT*
    - Mutants have an earlier flowering phenotype

## What features distinguish domestication genes?

### 1. The gene is located at a convergent point in a network

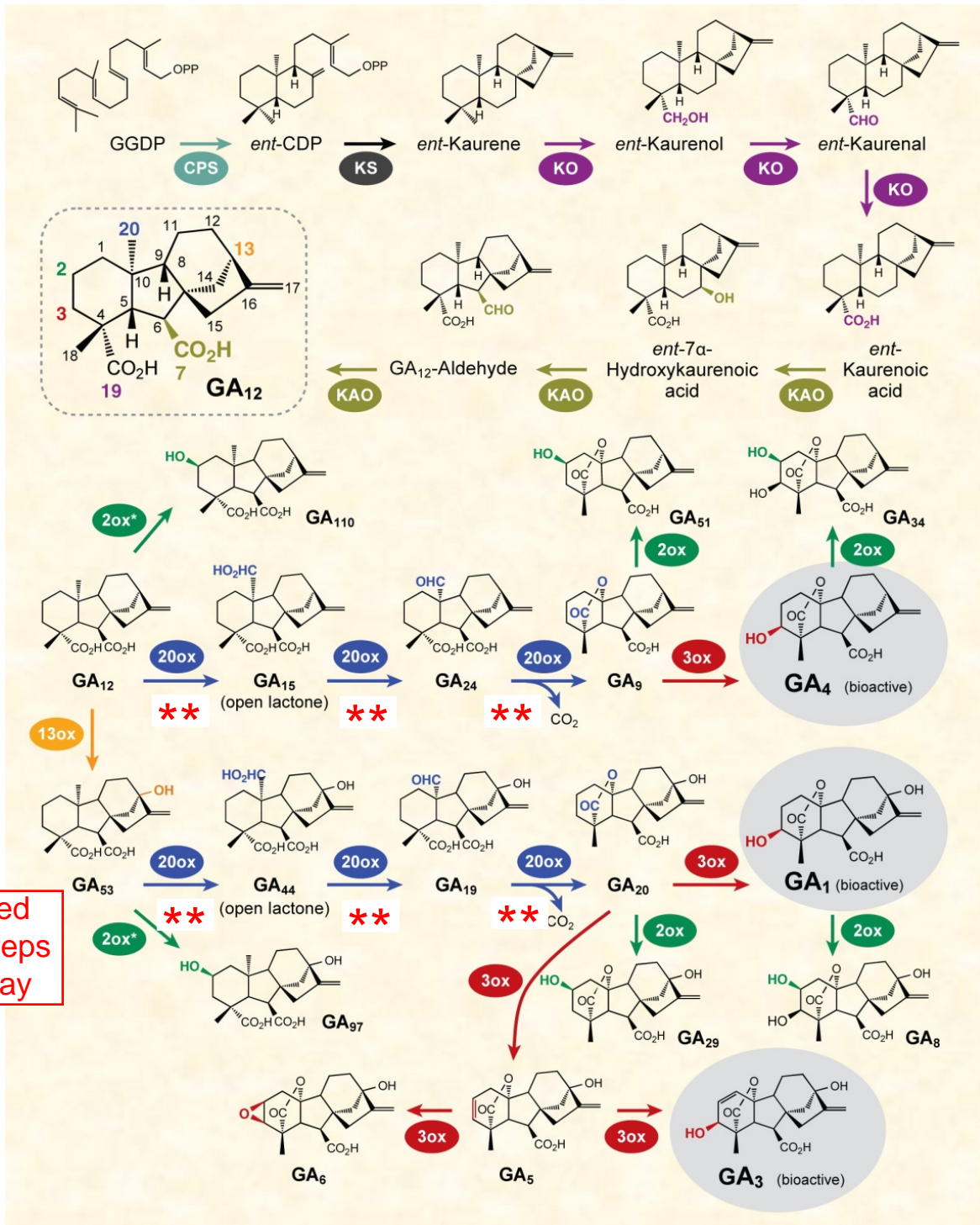
- *FT*, the evolutionary conserved florigen gene
  - Florigen is a universal inducer of flowering in angiosperms
  - Occupies a central point where multiple flowering cues converge.
  - It is then transported to floral meristems to stimulate flowering.

### 2. The gene is a critical member of a simple metabolic pathway.

- *GA20-oxidase*, critical enzyme that produces multiple GA types including the active GA<sub>1</sub> hormone.
  - A key enzyme in the gibberellic acid pathway.
  - Required to produce the active gibberellin requires for cell growth and stem elongation.

# The Gibberellic Acid Biosynthetic Pathway

- Many steps that can be mutated



Yamaguchi S. 2008.  
Annu. Rev. Plant Biol. 59:225–51.

# IMPORTANT QUESTION FOR DOMESTICATION STUDIES

- Did genomes evolve to have different solutions to achieving the same phenotype OR is the repertoire of genes limited within large taxonomic divisions of multiple plant species?

## Examples of a domestication trait control by different genes

### Reduced height

- **Wheat: *Rht-1***
  - Associated with Green Revolution
  - The gene is a ***Repressor of gibberellic acid pathway*** \*\*\*\*
    - Semi-dwarf allele has greater repression and leads to dwarf plants
- **Rice: *OsGA20ox***
  - Associated with Green Revolution
  - The gene is a ***Gibberellin pathway gene*** \*\*\*\*
    - Converts precursor into active form of GA
- **Sorghum: *dw3* AND maize: *br2***
  - The gene ***Modulates the transport of auxin*** \*\*\*\*
    - Maize allele critical to corn industry
- **Demonstrates multiple solutions to a common phenotype!!!**

### 3. The pleiotropic effects of a domesticated gene are minimal.

#### Flavonoid pathway genes

- Controlled by a ternary protein complex
  - Each protein is member of a transcription factor family with many members
  - Each member is selected for a specific function
  - Unlikely any one family member will have many functions.
  - Selection on any one gene will have minimal pleiotropic effects.
- Members of ternary complex
  - Myb-protein
  - Beta helix-loop-helix protein
  - WD40 protein (also WDR )
- Mutants in many species
  - Myb-protein
  - $\beta$ -HLH factor
- Mutants rarely seen
  - WD40 protein (WDR)

Multiple gene targets to change flower seed color!!!

**Table 1. Examples of molecular convergence underlying domestication-related phenotypic changes**

<b>Crop species</b>	<b>Phylogenetic distribution</b>	<b>Orthologous gene(s)</b>	<b>Class of gene product</b>	<b>Phenotypic effect</b>	<b>Causative changes</b>
Rice, barley	Species/family	OsGA20ox-2 (GA20 oxidase-2), HvGA20ox-2	Metabolic enzyme	Dwarfism	Coding
Wheat	Species	Rht-1 (reduced height-1)	SH2-TF	Dwarfism	Coding
Sorghum, pearl millet	Family	dw3 (dwarfing3), d2	Transporter protein	Dwarfism	Coding
Tomato, soybean, common bean	Family/above family	SP (SELF-PRUNING), Dt1 (determinate stem locus 1), PvTFL1y (TERMINAL FLOWER 1)	Signaling protein	Determinate growth	Coding
Barley, pea, strawberry	Above family	HvCEN (CENTRORADIALIS), PsTFL1c, FvTFL1	Signaling protein	Variation in flowering time	Mixed
Barley, wheat, ryegrass (Lolium perenne)	Species/family	VRN1 (BM5, TmAP1, WAP1, LpVRN1)	MADS domain TF	Variation in flowering time	Non-coding
Barley, wheat	Species/family	VRN2 (ZCCT1)	Zinc finger–CCT domain TF	Variation in flowering time	Mixed
Rice, barley, wheat, sorghum, sugar beet	Species/family/above family	OsPRR37 (pseudoresponse regulator protein 37), Ppd-H1, Ppd1, SbPRR37, BvBTC1	Regulator of the circadian clock pathway	Variation in flowering time	Mixed
Turnip, Brassica oleracea	Family	BrFLC2 (FLOWERING LOCUS C), BoFLC2	MADS domain TF	Variation in flowering time	Mixed
Rice, barley, pea, lentil	Family/above family	Hd17 (Heading date 17), EAM8 (EARLY MATURITY 8)/Mat-a (Praematurum-a), HR (HIGH RESPONSE TO PHOTOPERIOD), LcELF3 (EARLY FLOWERING 3)	Regulator of the circadian clock pathway	Variation in flowering time	Coding
Rice, wheat, sunflower, barley	Family/above family	Hd3a (Heading date 3a), VRN3/TaFT (FLOWERING LOCUS T), HaFT1, HvFT	Signaling protein	Variation in flowering time	Mixed
Rice	Species	Hd1 (Heading date 1)	Zinc finger TF	Variation in flowering time	Coding
Sorghum, rice, corn	Family	Sh1 (Shattering 1), OsSh1, ZmSh1	YABBY-like TF	Shatter resistance	Mixed
Rice, wheat, corn, foxtail millet, barley, amaranth, sorghum, broomcorn millet	Species/family/above family	GBSSI (granule-bound starch synthase 1)/Waxy	Metabolic enzyme	Glutinous seeds	Mixed
Rice, soybean	Species/family	BADH2 (betaine aldehyde dehydrogenase gene 2), GmBADH2	Metabolic enzyme	Fragrance	Coding

Rice, potato	Species/above family	Rd/DFR (dihydroflavonol-4-reductase), DFR	Metabolic enzyme	Coloration	Coding
Blood orange	Species	Ruby	MYB-TF	Coloration	Non-coding
Rice	Species	Bh4 (Black hull4)	Transporter protein	Coloration	Coding
Soybean	Species	R	MYB-TF	Coloration	Coding
Pea, potato	Above family	F3'5'H (flavonoid 3',5'-hydroxylase)	Metabolic enzyme	Coloration	Mixed
Rice	Species	Rc	bHLH-TF	Coloration	Coding
Grapevine	Species	VvMYBA1-3	MYB-TF	Coloration	Mixed
Corn, pearl millet, barley	Family	tb1 (teosinte branched 1), Pgtb1, INT-C (INTERMEDIUM-C)	TCP-TF	Plant architecture	Mixed
barley	Species	VRS1 (six-rowed spike 1)	Homeodomain-TF	Plant architecture	Coding
Rice, corn	Family	GS3 (QTL for grain size and length on chromosome 3), ZmGS3	Putative transmembrane protein	Grain size	Mixed
Rice	Species	GS5 (QTL for grain size and length on chromosome 5)	Metabolic enzyme	Grain size	Non-coding
Rice, corn, wheat	Family	GW2 (QTL for grain weight on chromosome 2), ZmGW2-CHR4/5, TaGW2	Metabolic enzyme	Grain size	Mixed
Rice, wheat	Species/family	Gn1a (QTL for grain number on chromosome 1, a)/OsCKX2 (cytokinin oxidase/dehydrogenase), TaCKX6-D1	Metabolic enzyme	Grain number	Mixed
Corn	Species	Opaque2	bZIP-TF	Grain quality	Mixed
Rice	Species	GW8 (QTL for grain weight on chromosome 8)/OsSPL16 (squamosa promoter-binding protein-like 16)	SBP-TF	Grain size and shape	Non-coding
Wheat, rye (Secale cereale)	Family	TaALMT1 (Al-activated malate transporter 1), ScALMT1	Transporter protein	Metal tolerance	Mixed
Sorghum, corn	Family	SbMATE1 (multidrug and toxic compound extrusion 1), ZmMATE1	Transporter protein	Metal tolerance	Mixed

Lenser and Theißen (2013) Molecular mechanisms involved in convergent crop domestication. Trends in Plant Science 18:704.