UNIVERSITY OF HOHENHEIM

History of domestication (Plants and humans)

3502-470 Plant Genetic Resources

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SS 2025

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The origins of agriculture

Sources of evidence

Theories of domestication centres

Global view of domestication

A synopsis of old world domestication

Domestication of humans

Reduced nutrient content

Domestication of agricultural landscapes

Why domestication?

Relationship between agriculture and domestication

> *The question must be raised:* Why farm? *Why give up the 20 hour work week and the fun of hunting in order to toil in the sun? Why work harder for food less nutritious and a supply more capricious? Why invite famine, plague, pestilence and crowded living conditions? Why abandon the Golden Age and take up the burden?*

Jack Harlan, 1992

Why is there agriculture?

Numerous theories try to explain the origin of agriculture:

- Godly gift
- Environmental determinist: Agriculture originated as a consequence of climate change
- Religious reasons
- Overpopulation
- Agriculture as discovery
- Extension of collecting, gardening
- Desire to make alcohol

(See 'Crops and Man' by Jack Harlan, 1992)

Godly gift

www.theoi.com

Demeter, the greek goddess of agriculture

Many mythologies of ancient cultures postulate a divine origin of agriculture.

Gods teach humans how to do agriculture.

Religous reasons for the origin of agriculture

- Key argument: It is difficult to predict the usefulness of domesticated animals *before* domestication ("Wild cattle for milk production? Wolves for herding sheep? No way")
- Hypothesis: Cattle was domesticated for ritual sacrifice.
- Many plants were used (and domesticated?) as well for ritual, ceremonial and magical purposes.

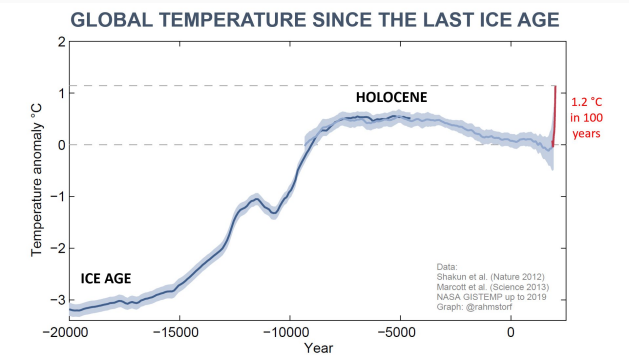
Religious reasons extended:

- 'Beer before bread'?
- But: Evidence that bread was used to make beer.
- Evidence for beer-making 5000 years ago (Sumerans).
- Experiment: Is it possible to make beer from wild barley?

Environmental determinist

- Agriculture arose due to climate change since the last ice age.
- Increased crowding due to drying up of fertile rangeland on restricted regions (Oasis theory).
- These development brought humans, plants and animals closer together, thereby leading to domestication (Propinquity theory).
- Events were accompanied by a shift from hunting and gathering to agriculture ⇒ Neolithic revolution

Temperature change before and during the Holocene

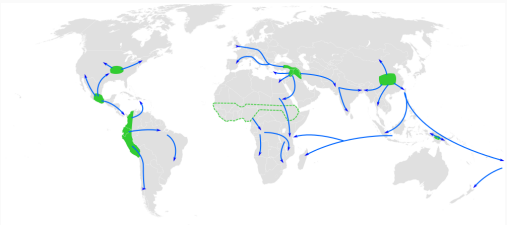


Source: Stefan Rahmstorf, https://twitter.com/rahmstorf/status/1220699044181368838.

Agriculture as discovery

- Traces back to Darwin, and has been more elaborated since then.
- States that cultivation of plants was an invention or a discovery ("Heureka!" model).
- No purpose is required just the accidential finding of plants that seem to be suitable for cultivation.
- There are several requirements for this theory. The most important is that humans were already **sedentary** before cultivation.

Centres of the origin of agriculture



Wikipedia

Radiocarbon dates:

- Fertile Crescent (11,000 BP)
- Yangtze and Yellow River basins (9000 BP)
- New Guinea Highlands (9000 -6000 BP)
- Central Mexico (5000- 4000 BP)
- Northern South America (5000 -4000 BP)
- Sub-Saharan Africa (5000 - 4000 BP, exact location unknown)
- Eastern USA (4000 -3000 BP)

Diamond and Bellwood 2003

Summary: Theories of agricultural origin

⇒ More theories in Wikipedia entry on Neolithic Revolution

Summary by Jack Harlan:

- More or less simultaneous origin in different regions
  → A single model may not suffice
- Higher population densities in agricultural societies
  → Agriculture is more work but feeds more people
- In agriculture, children are an asset
  → Labour force, etc.
- Vicious circle: More people need more food, hence more children are necessary.
- Surplus of food allows division of labour.

Sources of evidence

- Archaeology
- Botany
- Genetics
- Chemistry
- Anthropology
- Agronomy
- Linguistics

- Archaeology of plant remains
- Living plants: Genetics, morphology, geographic distribution → Domestication syndrome

Archaeological studies

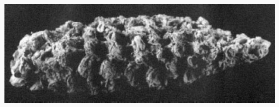
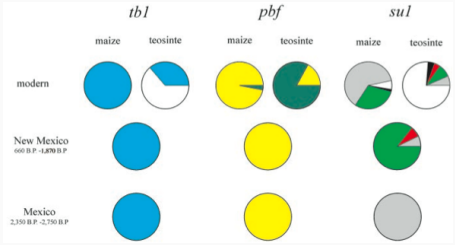
(A)  (B) 

Figure 1: (A)An ancient maize cob from Ocampo Caves, Mexico. The cob was dated to be 3890 years old and has a length of 47 mm. (B) Reconstruction of an early ear of corn from San Marcos Cave in the Tehuacán Valley, Mexico.

Smith 1995

Analysis of ancient DNA



Evidence from living plants

- What are the key morphological, physiological, chemical and genetic changes?
- What is the type (chromosomal, protein, DNA polymorphisms), level and geographic pattern of genetic variation?
- Which adaptations of wild ancestors have been lost in domesticates? Which adaptations are new in crops?
- What is the geographic distribution of wild ancestors?

Pioneers in the study of crop domestication and history

- Charles Darwin (1809-1882)
- Alphonse de Candolle (1806-1893)
- Nikolai I. Vavilov (1887-1943)
- Jack R. Harlan (1917-1998)

Alphonse de Candolle (1806-1893)

- French-swiss botanist
- Book: “Origin of cultivated plants” (1883)
- Used many types of information (botanical, archaeological, historical, linguistic)

Nikolai Vavilov (1887-1943)



- Russian geneticist
- Established the first gene banks
- Developed the theory of centres of crop diversity based on the taxonomical-geographical method

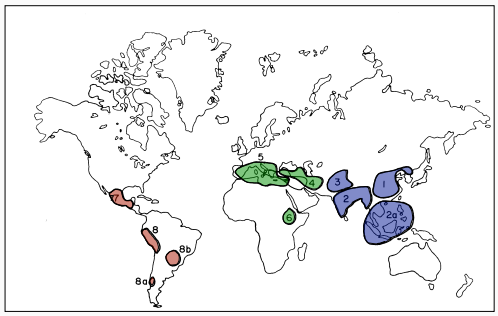
Centres of diversity

"In spite of the internationalization of cultivated crops and in spite of all the human migrations and colonizations as well as the very antiquity of agriculture, it is still possible ... to establish regions of endemic varieties and races, to discover regions where the maximum primary variation of strains occurred and to establish a number of regularities concerning the distribution of inherited characteristics."

Differentiation, taxonomical-geographical method

- Differentiate a plant into Linnean species.
- Determine the geographic distribution areas of these species.
- Determine in detail the composition of the varieties and races of each species and the inheritance of genetic variability.
- Establish the geographic distribution of inherited variation and determine the geographic centre of accumulation of varieties.

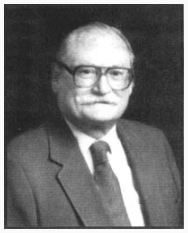
Centres of crop biodiversity



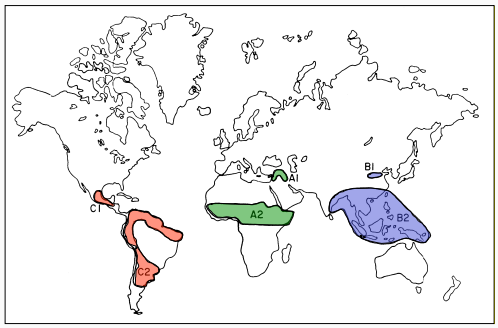
Further ideas of Vavilov

- Wild ancestors deserve much research effort.
- Include information from archaeology, history and linguistics.
- Centre of origin of cultivated plants is often correlated with diversity centre of associated pathogens.
- Distinguish between primary and secondary centres of diversity.

Jack Harlan (1917-1998)



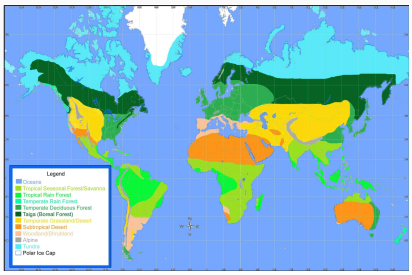
Centres and non-centres after Harlan



Harlan 1971

Map of world biomes

Harlan (1992): Some biomes are more conducive to domestication than others.



Wikipedia

Classify biomes according to their potential for agriculture

- **Tundra, taiga:** None
- **Temperate prairies:** Sunflower
- **Temperate steppes:** Proso millet, foxtail millet, hemp, *Triticum tauschii:* Donor of the *D* genome of bread wheat (*AABBDD*)
- **Tropical rain forest:** Sugarcane, banana and plantain, orange, mango, cacao
- **Deserts:** Data palm
- **Temperate forest:** Fruits and nuts like apple, pear, cherry, grape, walnut
- **Tropical highlands:** Principally Andes with root crops such as potato, East Africa with Arabica coffee
- **Sea coasts:** Coconut, cabbage, beet, cotton
- **Mediterranean woodlands and tropical savannas:** These biomes are of particular importance.

What is special about grasslands and mediterranean woodlands?

- They provided more then 50% of the major crops.
- The have a long dry season either in the summer (Mediterranean woodlands) or in the winter (savanna).
- Mediterranean woodlands provided wheat, barley, pea, rapeseed.
- Savannas provided mostly seed annuals or tuberous perennials; the tuber remains dormant during the dry season. Crops include maize, rice, sorghum, cassava, sweet potato, bean, peanut, yams.

Geographic origin of crops

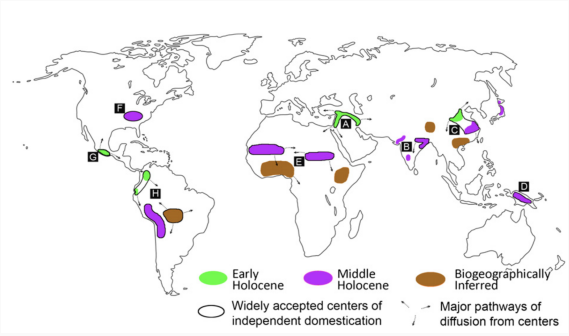
Region	Crops
North America	Sunflower, strawberry, grapevine, tobacco
Central America	Maize, Amaranth, Phaseolous, sweet potato, cassava, cotton, paprika, tomato, cocoa
South America	Amaranth, peanut, phaseolus bean, lupine, cassava, poatato, cotton, pineapple, pepper
Southeast Asia, India, Pacific region	Rice, yam, coconut, orange, banana, various spices
China	Rice, soja, yam, rapeseed, apricot, peach, cabbage, tea
Africa	Rice, pearl millet, sorghum, tef, oil palm, water melon, sesame, coffee
Near East	Wheat, barley, rye, oat, pea, lenses, lupines, rapeseed, olive, walnut, date palm, almond, apple, grapevine, plum, peach, onion

Ecological and genetic aspects of crops

Crop	Million tons	Annual/ Perennial	Ecology	Self-/cross-fertilizing	Ploidy
Wheat	468	A	Mediterranean woodlands	S	2,4,6
Maize	429	A	Tropical savanna	C	2
Rice	330	A	Tropical savanna	S	2
Barley	160	A	Mediterranean woodlands	S	2
Soybean	88	A	Woodlands	S	2
Sugar cane	67	P	Tropical forest	W,C	many
Sorghum	60	A	Tropical savanna	S	2
Potato	54	A	Tropical highland	W,C	2,4,6
Oat	43	A	Mediterranean woodlands	S	2,4,6
Cassava	41	P	Tropical savanna	W,C	4
Sweet potato	35	A	Tropical savanna	W,C	6
Sugar beet	34	A	Coastal	C	2,3,4
Rye	29	A	Mediterranean woodlands	C	2
Millets	26	A	Tropical savanna	C,S	2,4
Rapeseed	19	A	Mediterranean woodlands	C	4,6
Beans	14	A	Tropical savanna	S	2

Table 1: Ecological and genetic properties of major domesticated plants. Source: Harlan (1992)

Dates of the origin of agriculture



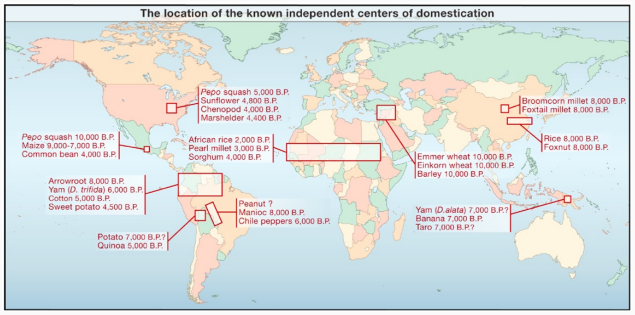
Larson et al., PNAS (2014)

Domestication dates

Time	Crop plant	Reproduction	Centre of origin
1000-today	Sugar beet	ob	Europe
2000	Rape seed (canola)	ob/ib	Mediterranean
3000	Sunflower	ob	North America
4000	Potatos	ob (clonal)	South America
5000	Oats	ib	Eastern Europe
	Hemp	ob	China
6000	Rye	ob	Turkey
	Millet	ib/ob/	China
	Rice	ib	China
7000	Bean (Vicia faba)	ob	Near East
8000	Cotton	ib/ob	Mexico
	flax, linen seed	ib	Near East
9000	barley	ib	Near East
	wheat	ib	Near East
	lentils	ib	Near East
	peas	ib	Near East

ob: outbreeding; ib: inbreeding

Summary: Centres of domestication



Doebley et al., 2006

Examples for the origin of crop plants

Southeast Asia, India, Pacific region

- Rice
- Yam
- Coconut
- Orange, banana
- Various spices

China

- Rice
- Soja
- Yam
- Rapeseed
- Apricot, peach
- Cabbage
- Tea

Geographic origin of crop plants

Africa

- Rice
- Pearl millet
- Sorghum, Tef
- Oil palm
- Water melon
- Sesame
- Coffee

Near East

- Wheat
- Barley
- Rye
- Oat
- Pea, lenses, lupines
- Rapeseed
- Olive
- Walnut, date palm, almond
- Apple, grapevine, plum, peach
- Onion

Relevant time periods

- Epipaleolithic/Mesolithic (20,000 to 9500 BCE)
- Neolithic (10,200 BCE)
- Bronze Age (3,300-1,200 BCE)

(BCE: Before the common era; 1,000 BCE → 3,020 years ago)

Early signs of domestication

- Earliest signs in prepottery Neolithic B (PPNB) farming villages.
- 10,500 - 10,100 BP
- Spikelet forks of emmer and einkorn wheat.
- Domestication trait: rough disarticulation scars → Nonshattering seeds that were threshed
- Single domestication event or multiple domestication events?

Brittle rachis as a diagnostic trait

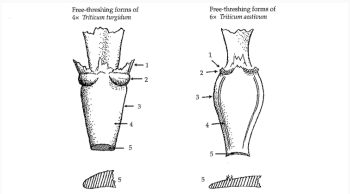


Fig. 5B The structure of the rachis fragment in tetraploid and in hexaploid free-threshing wheats, pointing out five diagnostic traits for distinguishing between 4X *Triticum turgidum* cultivars (excluding cavifolium forms) and 6X *T. aestivum* cultivars (Hillman 2001, and pers. comm.).

Diagnostic traits	Tetraploid free-threshing wheats	Hexaploid free-threshing wheats
1. lower part of the glumes	Usually retained after threshing, including the lower part of the keel	Deciduous and fully removed by threshing
2. Shape of the glume base	A prominent lump is present beneath each glume base	The lump is missing (or is only very rudimentarily developed)
3. Shape of the rachis internode	The sides of the internodes are more or less straight, and converge gradually downwards	The sides of the internodes are curved
4+5. Structure of the edge of the internode	The internode is relatively thick, smooth, with rounded edge	The edge is thinner, grooved by a fine longitudinal furrow, with ridges frequently supporting short hairs

Zohary et al., 4th Edition (2012)

Founder crops of Old world agriculture

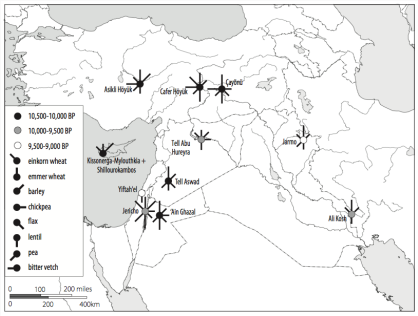
Common Name	Scientific Name	Wild ancestor
Cereals		
Emmer Wheat	*Triticum turgidum* subsp. *dicoccum*	*T. turgidum* ssp. *dicoccoides*
Einkorn wheat	*T. monococcum* ssp. *monococcum*	*T. monococcum* ssp. *boeoticum*
Barley	*Hordeum vulgare*	*H. spontaneum*
Pulses		
Lentil	*Lens culinaris*	*Lens orientalis*
Peas	*Pisum sativum*	*Pisum humile*
Other crops		
Flax	*Linum usitatissimum*	

Patterns of domestication

- Cereals were domesticated before the legumes → Transition to agriculture started with cereals
- Other, minor founder crops:
  - Bitter vetch (*Vicia ervilia*)
  - Chickpea (*Cicer arietinum*)
- Taxonomic classification change quite frequently.
- What is a species and a subspecies?

(a) *Vicia ervilia* **(b)** *Cicer arietinum*

Archaeological sites in the Fertile Crescent



Zohary et al., 2012

Neolithic food production

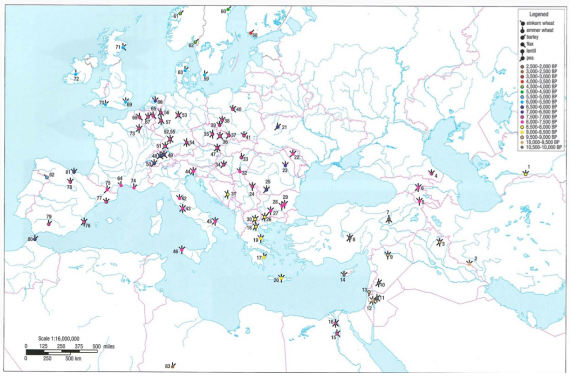
- Food package: at least one cereal, one legume and flax
- Neolithic food production package: Vegetative crops and animals

Rapid transition to agriculture

- 10,500 - 10,200 BC: First farming in the Levantine corridor
- 9,500 - 9,000 BC: Farming throughout the whole Fertile Crescent
- 9,000 - 8,500 BC: Agriculture has spread to Greece and Crete
- 8,000 BC: Agriculture in Bosnia-Hercegovina and Turkmenia (Turkmenistan); further spread to Spain and South Italy
- 7,500 BC: Evidence for agriculture is established throughout central Europe from Northern France over Germany to Poland

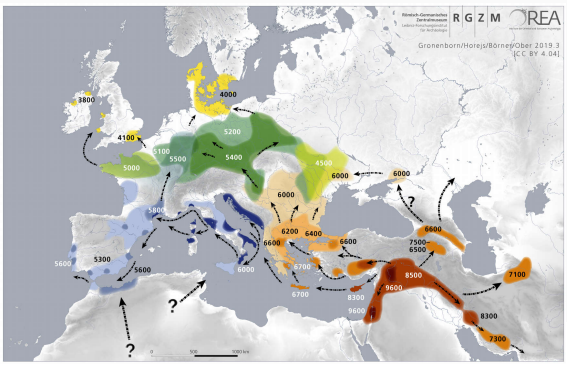
Much less is known about Central Asia: Lesser density of archaeological sites

Spread of agriculture outside the Fertile Crescent



Zohary et al., 2012

Spread of agriculture from the Fertile Crescent



Römisch-Germanisches Zentralmuseum

Secondary domestications

- Domestications outside the core area
- Poppy (*Papaver somniferum*): Western Europe
- Chufa (*Cyperus esculentus*): Nile region
- Broomcor millet (*Panicum milliaceum*): Caspian basin

Papaver

Domestication of fruit trees

- Early domestication from 6,800 - 6,300 BC in period of Calcolithic levant
- Olive, grapevine, fig and date palm
- Since 4,500 BC these trees are very abundant
- Apple, pear, plum and cherry are much later, after 1,000 BC

Implications of fruit tree domestication

- First signs of domestication in Fertile crescent
- Fruit tree domestication after cereal domestication
- Vegetative propagation (grafting): New invention
- Simultaneous domestication of several fruit trees
- Long-term investment: Requires fully sedentary lifestyle
- Rapid spread outsite of Fertile Crescent

Domestication of vegetables

- Little known about vegetable domestication: Soft tissues!
- In the Nile valley, garlic, leek, onion, lettuce, melon, watermelon were cultivated at 1,000 BC.
- But in the Bronze age, vegetables were an important part of the food production system.

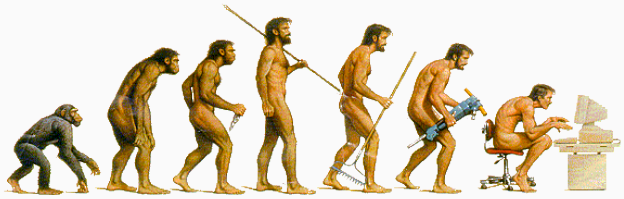
Secondary domestication: From weed to crop

- Weeds that accompany crops
- Secondary domestication: Either on purpose or by natural selection
- Natural selection: Nonshattering genotypes were accidentally selected with the harvested grains
- Examples: Rye (*Secale cereale*, oat (*Avena sativa*), gold of pleasure (*Camelina sativa*)

Wikipedia

The human domestication syndrome

Yes, we are domesticated too...



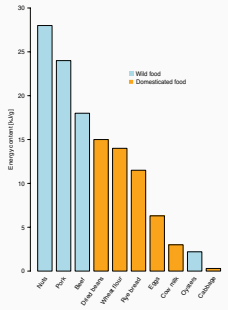
Yes, we are domesticated too...

The domestication of humanity

Main effects of agriculture

- a tendency towards a sedentary life style
- a narrower, mainly cereal-based diet
- more crowded conditions
- smaller and less robust body, especially in the facial area

Lower energy content of 'domesticated food'

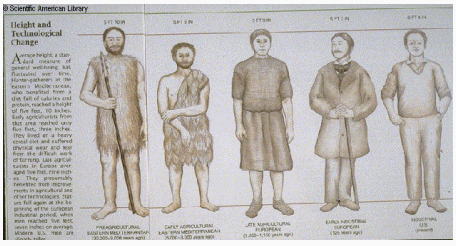


Reichholf, *Warum die Menschen sesshaft wurden* (2008)

Health effects of agriculture

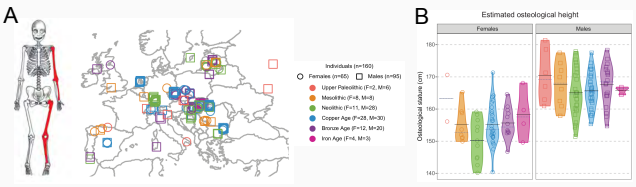
- Vitamin deficiencies
- Hypoplasia of tooth enamel
- Dental caries
- New diseases: anthrax, salmonellosis...
- Famines: Plant pathogens adapt to agricultural practices
- Food poisoning: Mycotoxins, etc.

Change of body size after domestication



- More diverse diet since 4000 BP.
- Same pattern in many agricultural societies.

Change of body size caused by environment, not genes



Source: Marciniak et al. (2021)

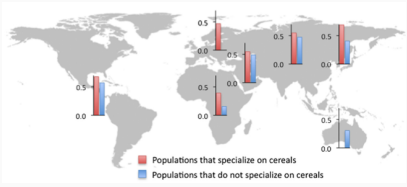
Joint analysis of morphology and ancient DNA: Neolithic body size reduction caused by environmental stress, not by allele frequency change.

Adaptation of humans to a new diet

Strong signals of natural selection:

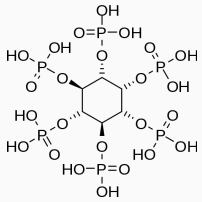
- Lactase gene: Digestion of cow milk
- Amylase gene: Digestion of starch

Change in allele frequencies of a SNP at the gene PRLP2:



Source: Hancock et al. (2010)

Nutrient deficiencies



- Phytates occur in many cereals
- Phytates bind minerals
- Reduced absorption in intestine

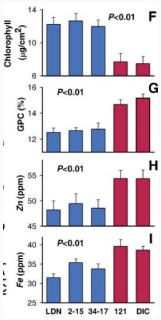
Reduction of micronutrients in grains by domestication

- Micronutrients were not targets of selection.
- Deleterious mutations and genetic trade-offs reduced micronutrient content.
- Seen in different cereal crops.

The NAM-B1 gene in wheat controls grain micronutrients

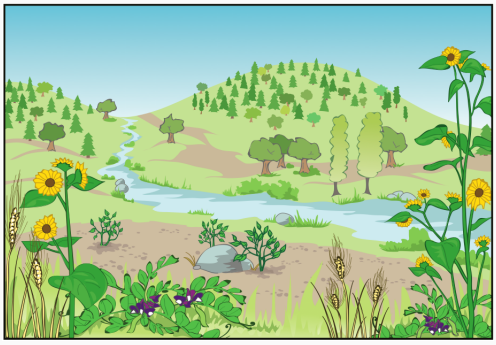
- NAM-B1 gene controls photosynthesis and senescence.
- Low micronutrient content is a pleiotropic effect.
- Wildtype allele found in:
  - 42 of 42 wild emmer accessions
  - 17 of 19 domesticated emmer wheat accessions
  - 0 of 57 durum wheat accessions
  - 0 of 34 hexaploid bread wheat

The NAM-B1 gene in wheat controls grain micronutrients

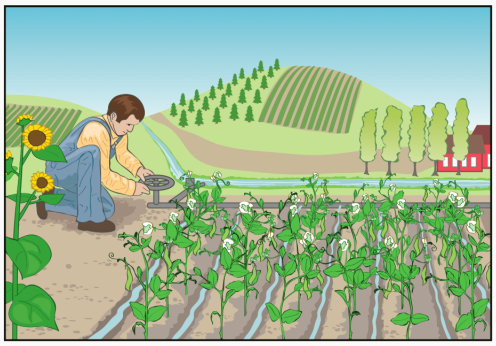


(a) Phenotypic variation between the two alleles observed at the *NAM-B1* gene in wheat. (b) A single nucleotide insertion into the protein-coding region causes the mutant phenotype in the *NAM-B1* gene. The red allele is the wildtype allele. Source: Uauy et al. (2006)

Evolution of agricultural landscapes



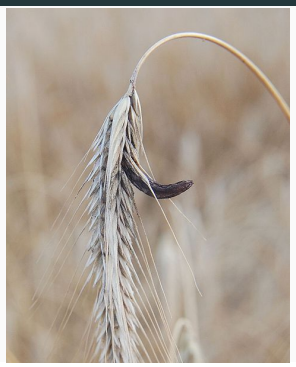
Evolution of agricultural landscapes



Domestication-associated evolution of fungal plant pathogens

Plant pathogen	Time scale
Mycosphaerella graminicola on wheat	10-12,000 years BP
Magnaporthe oryzae on rice	7000 years BP
Phytophthora infestans on potato	7000 years BP
Ustilago maydis on maize	8000 years BP

Ergotism (St. Anthony's Fire)



Wikipedia

Wikipedia

Fusarium

Variety 'Blanco de Urubamba' with and without Fusarium

Fusarium

Selection of 'noninfected' grains by indio woman

Summary

- There are numerous explanations for the origin of agriculture. Most likely none of them explains all transitions to agriculture and neither a single explanation is sufficient.
- Different types of evidence such as archaeology, distribution of crops and genetics are used to define theories of domestication.
- Vavilov and Harlan defined centres of diversity and domestication of crop plants.
- These centres originated in different times in history.
- Humans are domesticated!
- Complex evolution of humans, agroecosystems, pathogens.

Further reading

- Jack Harlan, *Of Crops and Man* 2nd edition, Chapters 1,2 and 7 [ILIAS]
- Zohary et al., Domestication of Plants in the Old World. 4th Edition (2012) Chapters 1-3

Two very good biographies of Nikolai Vavilov:

- Peter Pringle, The Murder of Nikolai Vavilov, Simon and Schuster (2008)
- Gary Paul Nabhan, Where our food comes from - Retracing Nikolay Vavilov's quest to end famine, Island Press (2009)

General summaries of the history of domestication:

- Bruce D. Smith, The emergence of agriculture, Scientific American Library (1995)
- Denis Murphy, People, plants and genes. Oxford University Press (2006), Chapters 1-3 and 9

Review questions (Domestication)

- Is it in principle possible to test whether the environmental determinist hypothesis for the origin of agriculture is true?
- Why is it unlikely that a single hypothesis explains all domestication events?
- What are the advantages of a religous reasons or the beer before bread hypothesis for the begin of the domestication rather than domestication for food? What are the disadvantages?
- Which reasons may cause the multiple origin of agriculture in different regions of the world?
- Which methods are used for studying the origin of agriculture? What are their advantages and disadvantages?
- Why and how does ancient DNA provide information about the origin and geographic location of domestication?

Review questions (Human Domestication)

- What are the key assumptions in the use wild crop relatives for analysing the DNA sequence as a crop?
- Why are genetic crosses between wild ancestors and modern crops useful for the identification of the true progenitor of a crop and domestication traits?
- What are the strengths and weaknesses of the Vavilov's method, of Harlan's megacentre and the biome theories for the identifying centres of domestication and crop plant diversity?
- Which factors determine in your opinion which plant became domesticated and which ones did not?
- How would you define the human domestication syndrome?
- Why is evolution (for example of host and pathogens) expected to occur more rapidly in simplified agroecosystems than in natural ecosystems?

References i

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content/10.1101/2021.03.31.437881v1, publisher: Cold Spring Harbor Laboratory Section: New Results

Uauy C, Distelfeld A, Fahima T, Blechl A, Dubcovsky J (2006) A NAC Gene Regulating Senescence Improves Grain Protein, Zinc, and Iron Content in Wheat. Science 314(5803):1298–1301, DOI 10.1126/science.1133649, URL https://www.sciencemag.org/lookup/doi/10.1126/science.1133649