Plant and Animal Domestication as Human-Made Evolution

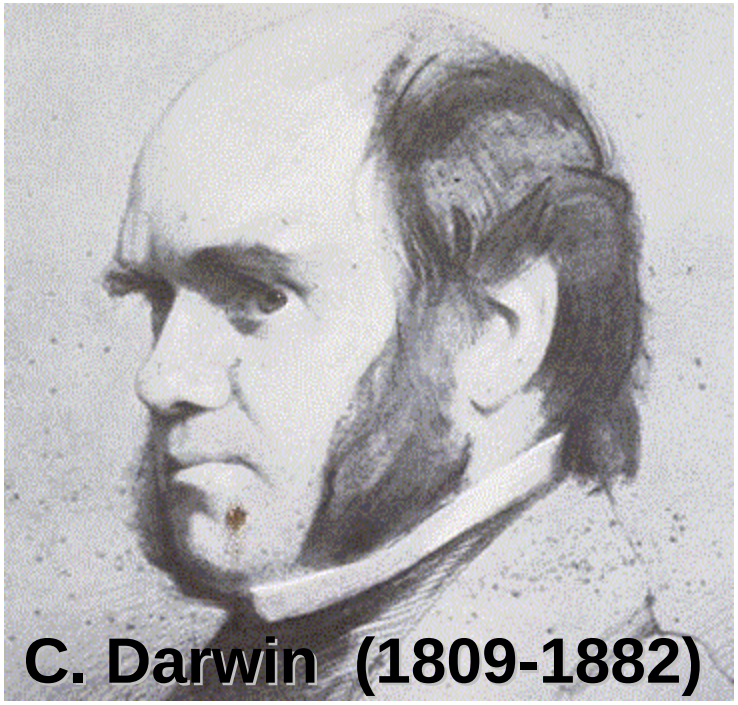
Paul Gepts
University of California, Davis
plgepts@ucdavis.edu

Introduction

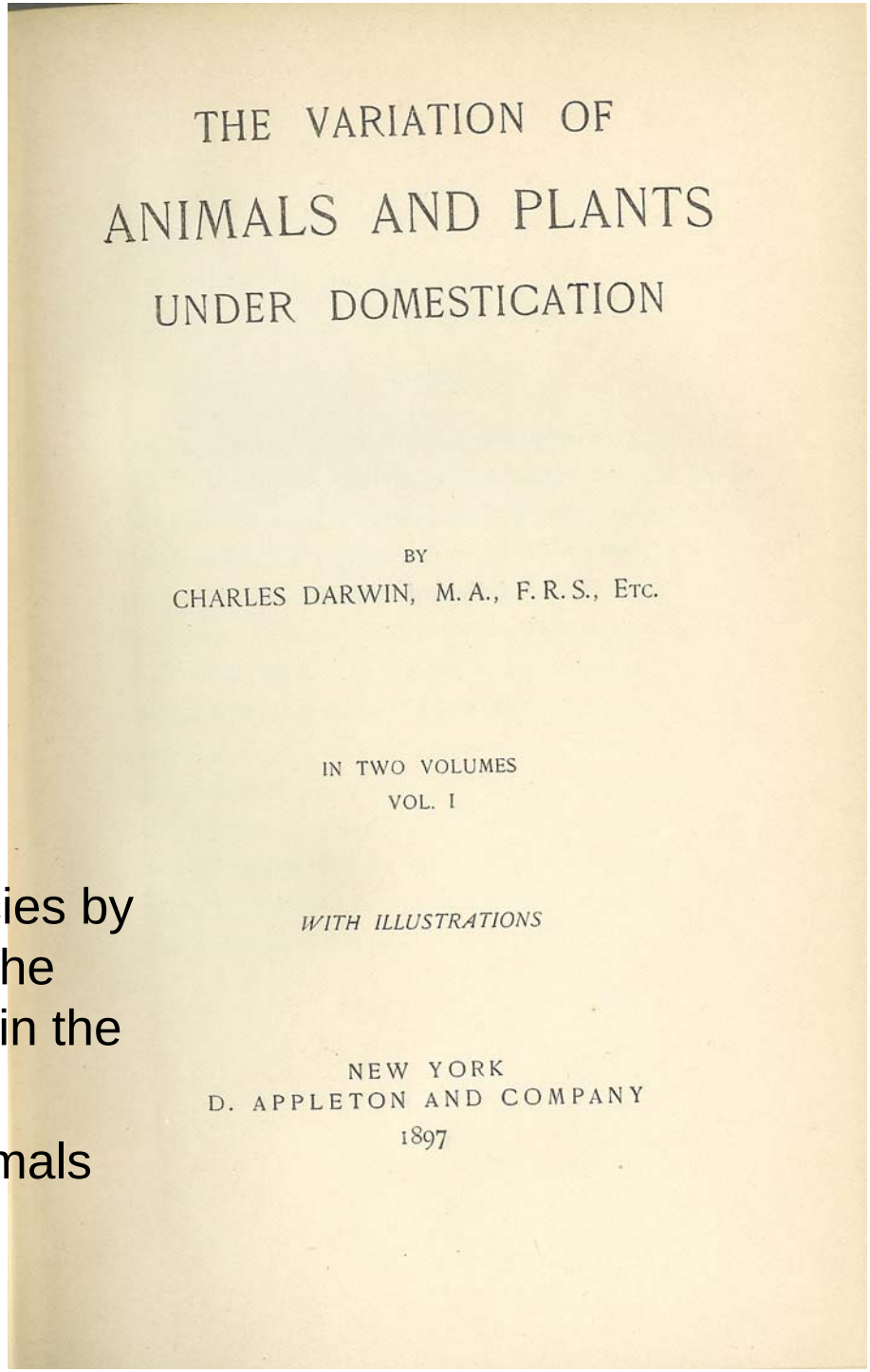
- Examples of the importance of evolutionary studies in agriculture and biotechnology
  - **Resistance management** in pesticide application and the conservation of valuable pest control tools
  - **DNA shuffling** and the production of more efficient enzymes
  - **Host-pest co-evolution** and the development of more resistant crops
  - **Crop and animal domestication** and evolution and the genetic improvement of crops and animal breeds

[... *No doubt man selects varying individuals, sows their seeds, and again selects their varying offspring ... Man therefore may be said to have been trying an experiment on a gigantic scale; and it is an experiment which nature during the long lapse of time has incessantly tried* ...]

C. DARWIN (1868), The Variation of Animals and Plants under Domestication



- Darwin's conundrum: "*The laws of inheritance are quite unknown*."
  - Chapter 1 of The Origin of Species by Means of Natural Selection or The Preservation of Favored Races in the Struggle for Life (1859)
  - The Variation of Plants and Animals under Domestication (1868)



THE VARIATION OF
ANIMALS AND PLANTS
UNDER DOMESTICATION

BY
CHARLES DARWIN, M. A., F. R. S., ETC.

IN TWO VOLUMES
VOL. I

WITH ILLUSTRATIONS

NEW YORK
D. APPLETON AND COMPANY
1897

Questions raised/Observations made by Darwin

- Evidence for selection and inheritance?
  - Gigantism of harvested organs: e.g.,
    - udders of cows and goats
    - seeds of domesticated plants
  - *"Comparing the diversity of leaves, pods, or tubers, or whatever part is valued in the kitchen-garden, in comparison with the flowers of the same varieties"*
  - "*Very many of the most strongly-marked domestic varieties could not possibly live in a wild state."*

- Observations about domestication
  - " *...in a vast number of cases, we cannot recognize ... the wild parent-stocks of the plants which have been longest cultivated in our flower and kitchen-gardens*."
  - *"In the case of most of our anciently domesticated animals and plants, I do not think it is possible to come to any definite conclusion, whether they have descended from one or several species*."; i.e. which is the wild ancestor(s), single or multiple domestications, where?

Evidence for Origin and Dispersal of Domesticated Plants and Animals

(modified from Harlan and de Wet 1973)

- **Plants & Animals**
  - Living:
    - Experimental taxonomy
    - Geographic distribution
    - Ecological distribution
    - Genetic systems
    - Variation patterns
    - Morphology, physiology
    - Genetic reconstruction
  - Dead:
    - Archaeology
    - Palynology
    - Paleobotany
- **Humans**
  - Living:
    - Language
    - Oral tradition, creation stories
    - Techniques
    - Attitudes towards the crop, animals
    - Nutrition
  - Dead:
    - History
    - Art
    - Archaeology
    - Physical anthropology

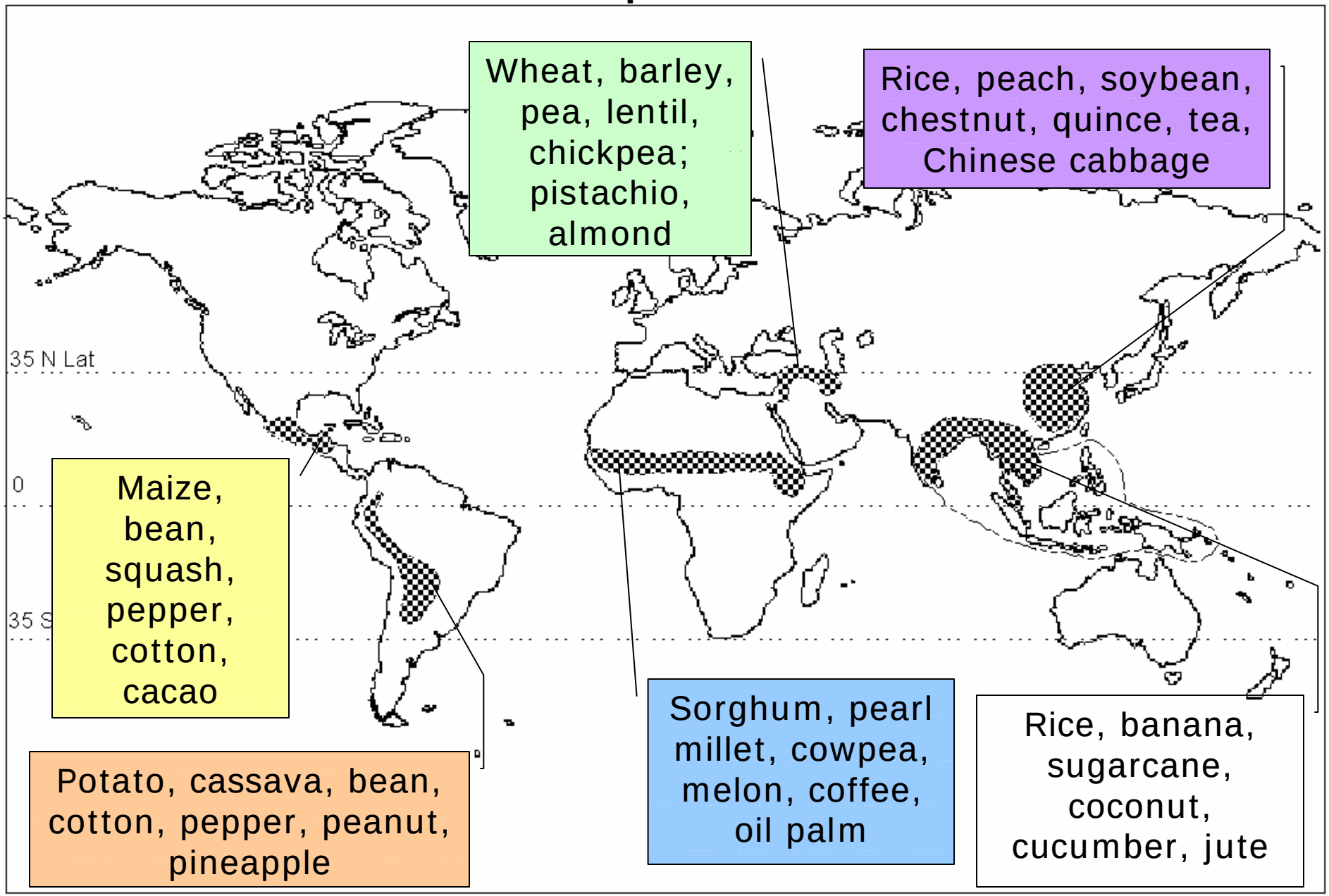
What is domestication?

- Definition of domestication: “Process by which wild plants or animals become adapted to humans and the environment they provide.”
- More than captive rearing or cultivation, taming
- Selection process leading to heritable morphological, physiological, genetic, and behavioral changes

Domestication as an Evolutionary Study System

- In many cases, wild progenitor (or its immediate descendant) and domesticated plant or animal exist
- Traits subject to selection have been identified (“domestication syndrome)
- Time frame is generally known (approx. 10,000 years)

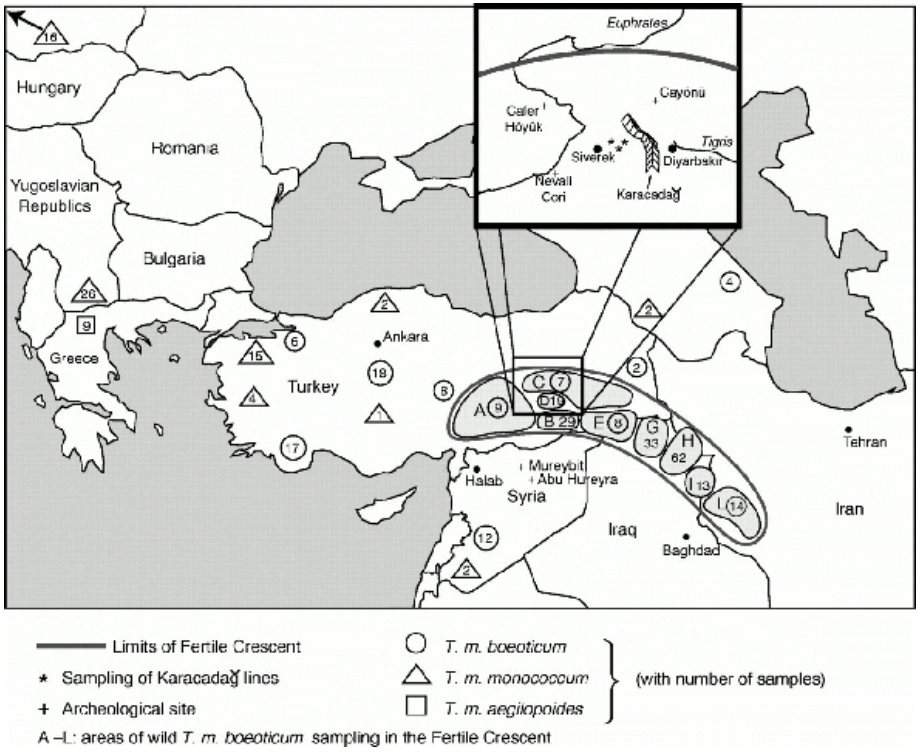
Centers of Domestication of Crop Plants



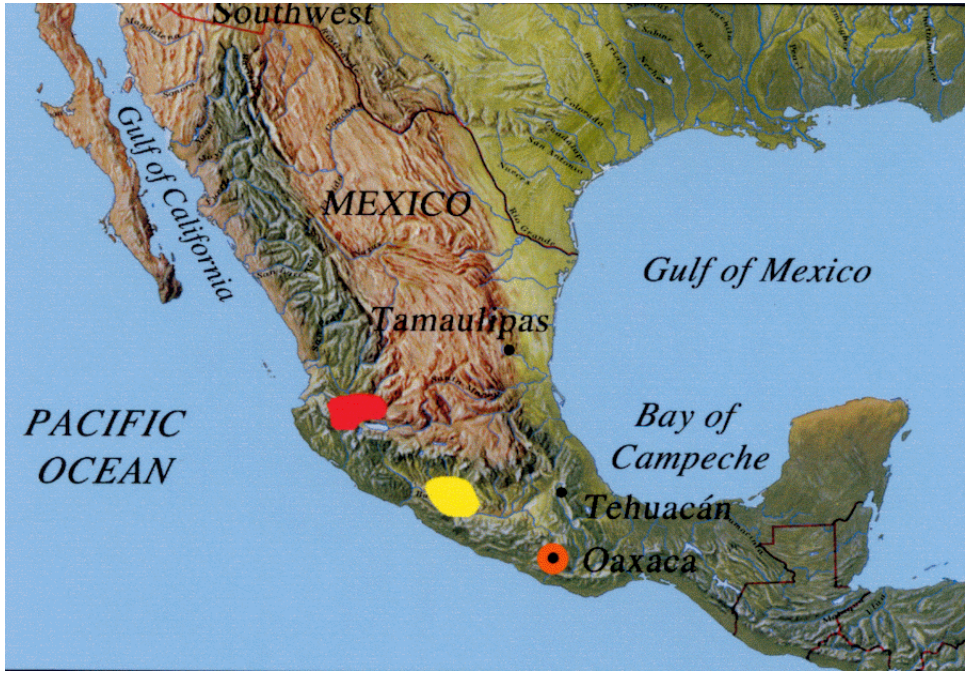
Gepts 2002, 2003

Putative Domestication Sites

Einkorn wheat

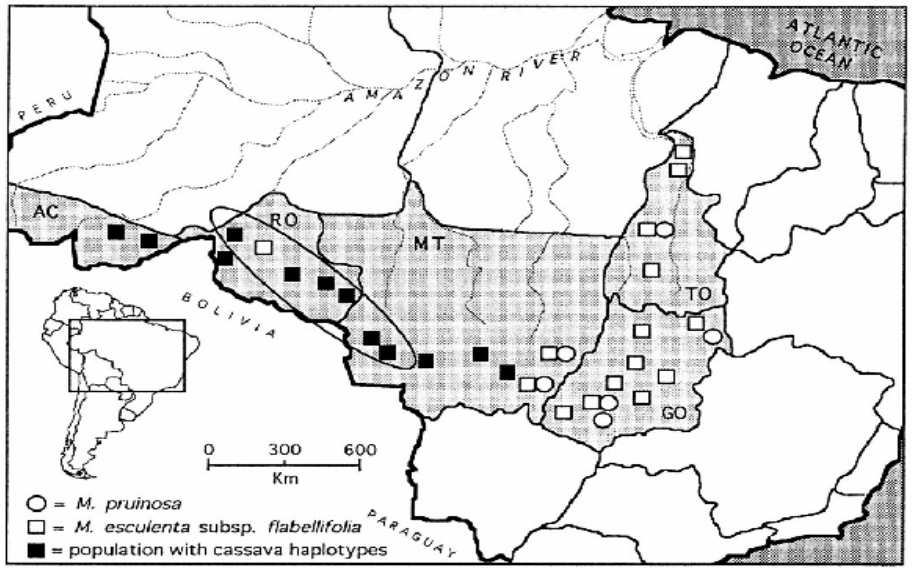


Heun et al. 1997



Bean, maize, squash

Smith 2001



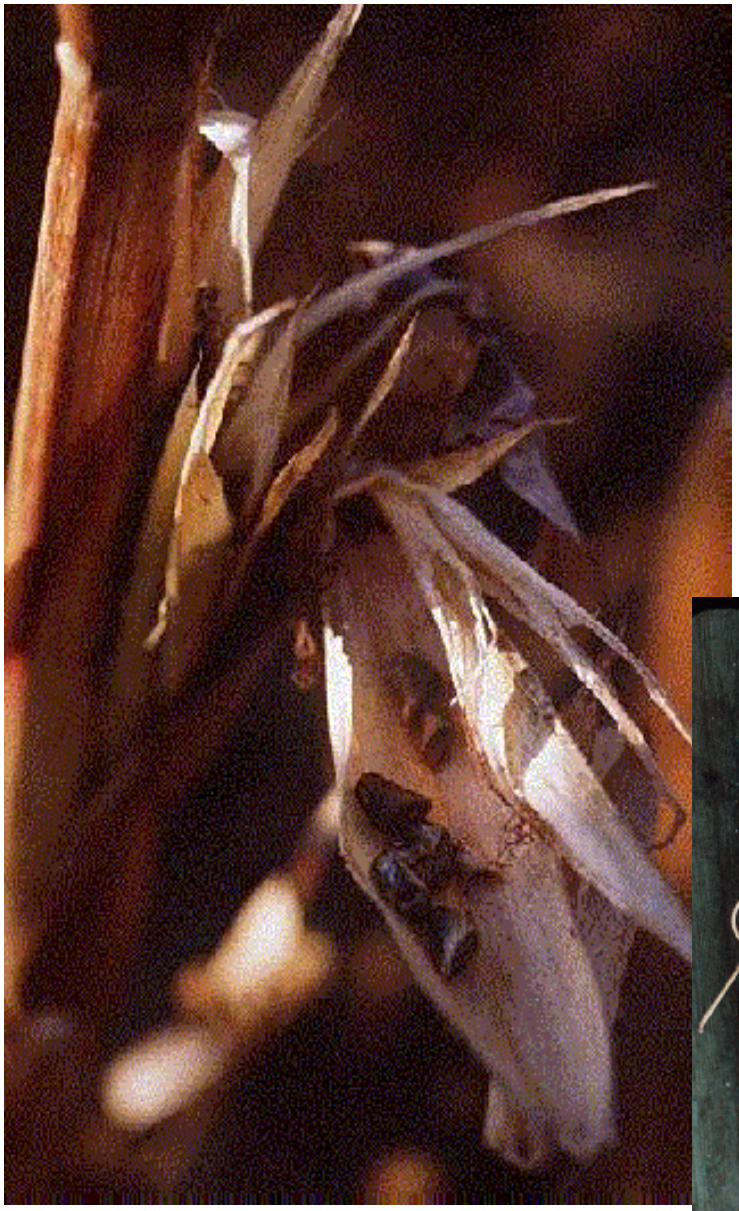
Cassava

Olsen and Schaal 1999

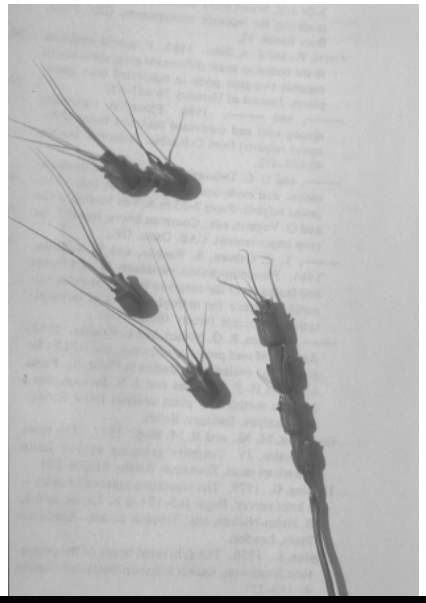
Domestication as an evolutionary study system

- In many cases, wild progenitor (or its immediate descendant) and domesticated plant or animal exist
- Traits subject to selection have been identified ("domestication syndrome)
- Time frame is generally known (approx. 10,000 years)

Seed Dispersal



Zea mays



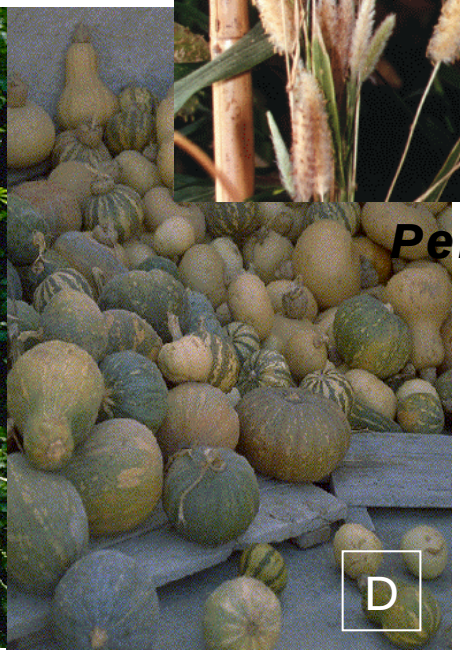
***Aegilops* sp.**

Phaseolus vulgaris

Increase in Size of Inflorescence, Fruit and/or Grain

Zea mays

Pennisetum glaucum

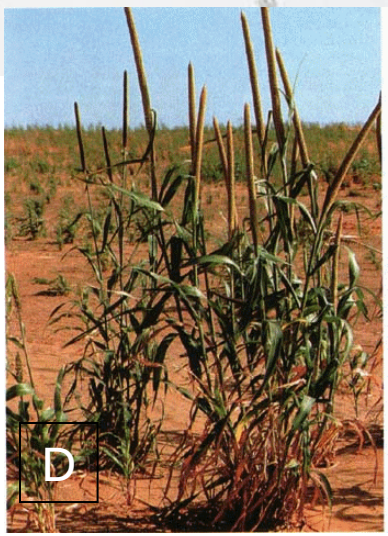


***Cucurbita* sp.**

Changes in Growth Habit

Zea mays

Phaseolus vulgaris



Pennisetum glaucum

P. Bruegel the Elder (1565)

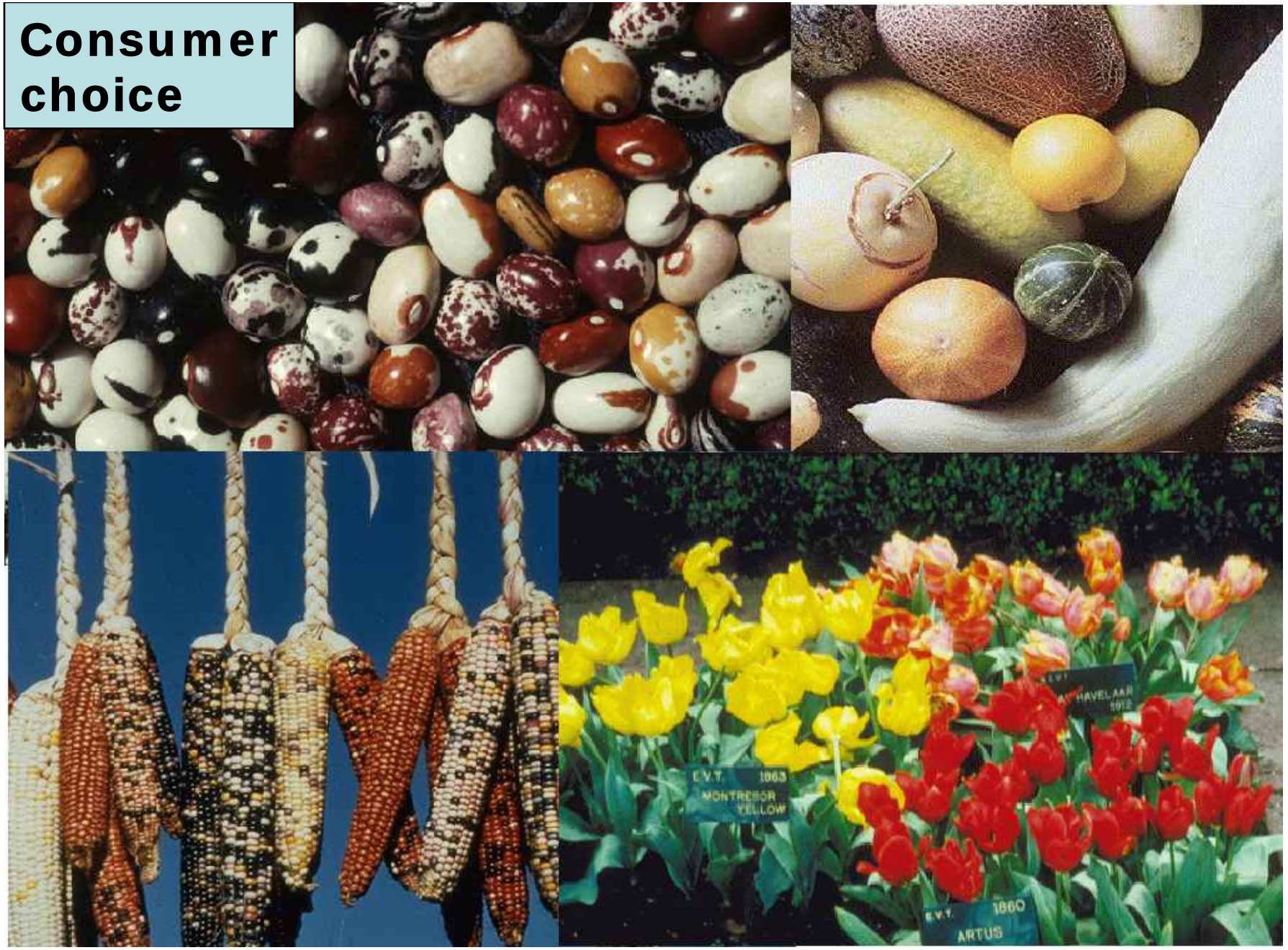
Photo: B. Bigbee (Utah State)

Gigantism

Frary et al. 2000

P. Gepts

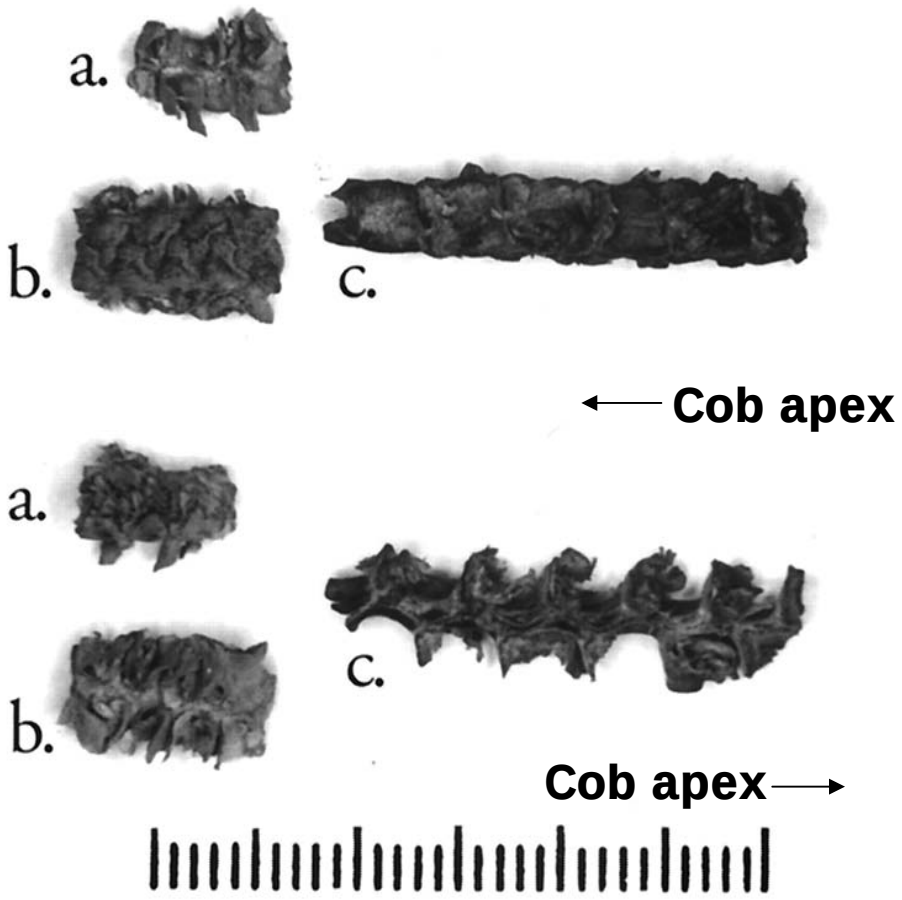
Consumer choice



From Gepts 2002a

Early Steps in Maize Domestication

- Stiff rachis
- Shallow cupules, perpendicular orientation of lower glumes
- Two or four rows of seeds:
  - a, b: Single spikelet/node
  - c: Two spikelets/node



(Guila Naquitz: 5,400 BP: Benz 2001)

Changes in Yield

- Evolution of wheat yields in Mesopotamia (Araus et al. 2001) :
  - c. 8000 BC: estimated grown yield was 1.56 Mg/ha
  - contemporary yields: roughly 1.0 Mg/ha
- Maize yields in U.S.A.
  - Flat until 20th century?

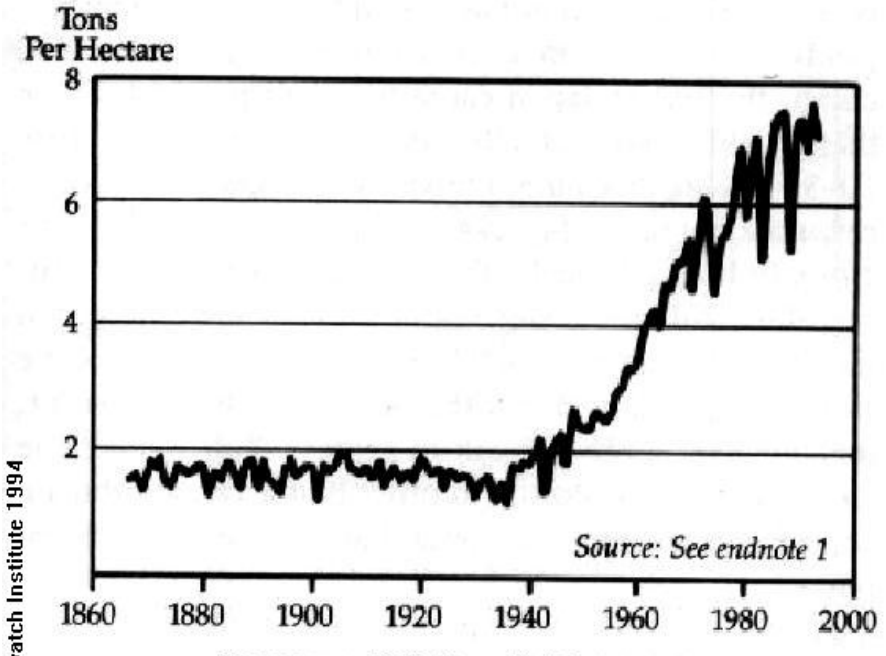


FIGURE 10-1. *U.S. Corn Yield, 1866–1993*

Domestication as an evolutionary study system

- In many cases, wild progenitor (or its immediate descendant) and domesticated plant or animal exist
- Traits subject to selection have been identified (“domestication syndrome)
- Time frame is generally known (approx. 10,000 years)

Time Frame of Domestication

Location	Crop[z]	Age (years BP)
Mesoamerica	Squash	10,000
	Maize	6,200
Fertile Crescent	Einkorn wheat	9,400-9,000
	Lentil[y]	9,500-9,000
	Flax[y]	9,200-8,500
	Goat[x]	10,000
	Pig[x]	10,000
China	Rice	9,000-8,000
Eastern United States	Squash	4,300
	Sunflower	4,300

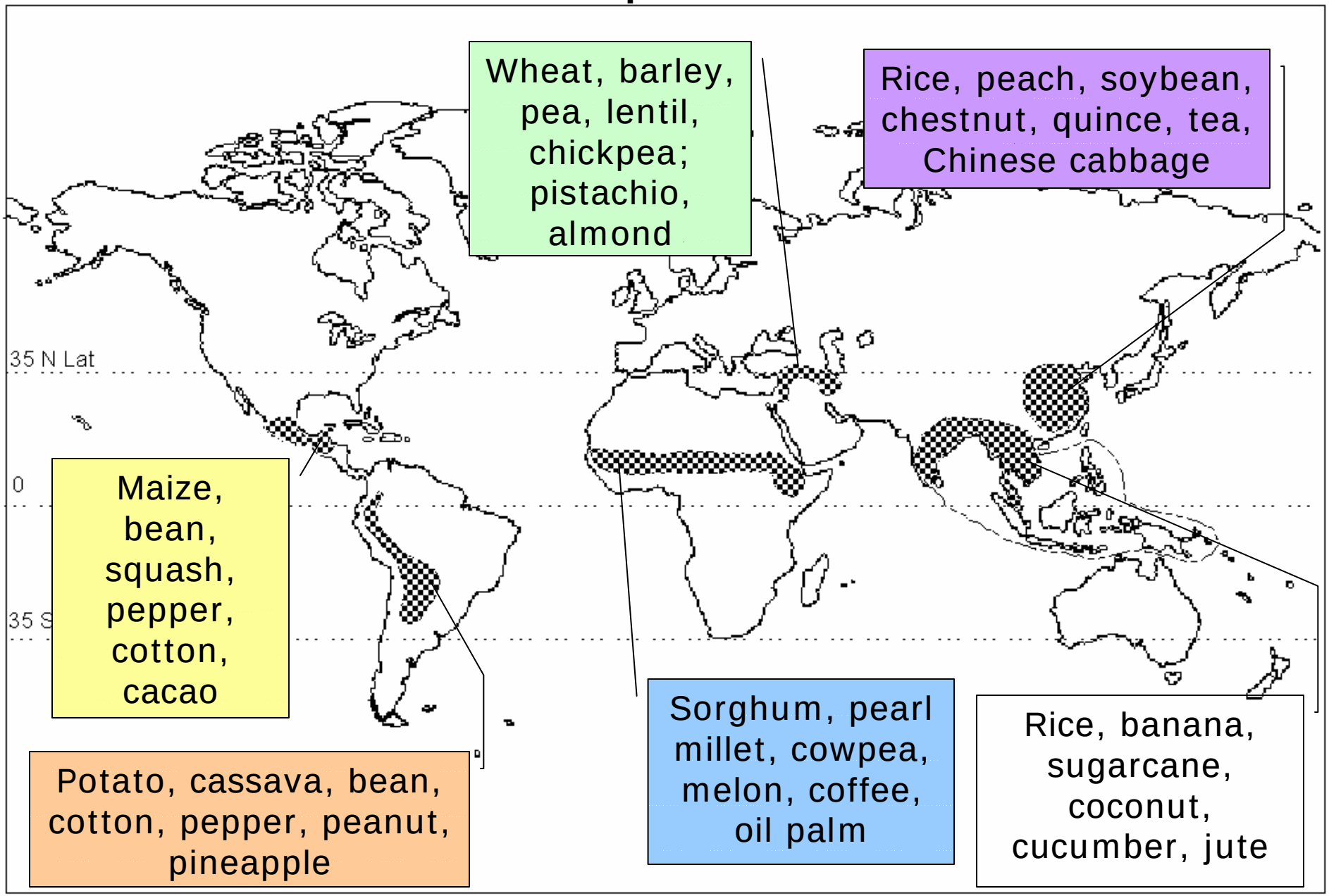
[z] Only the earliest domesticated crop remains are listed
[y] Uncertainty as to the domestication status
[x] Additional centers of domestication for the goat (in the Indian subcontinent) and the pig (in Eastern Asia) have been postulated

Gepts 2004

Major Findings about Domestication

- **Multiple, independent origins** of plant and animal agriculture in last 10,000 years
- **Genetic bottlenecks** in genetic diversity
- Important role of **genes with major phenotypic effect**
- Are genes for domestication **clustered?**
- **Molecular function** of genes for domestication
- Is there a **potential for domestication?**

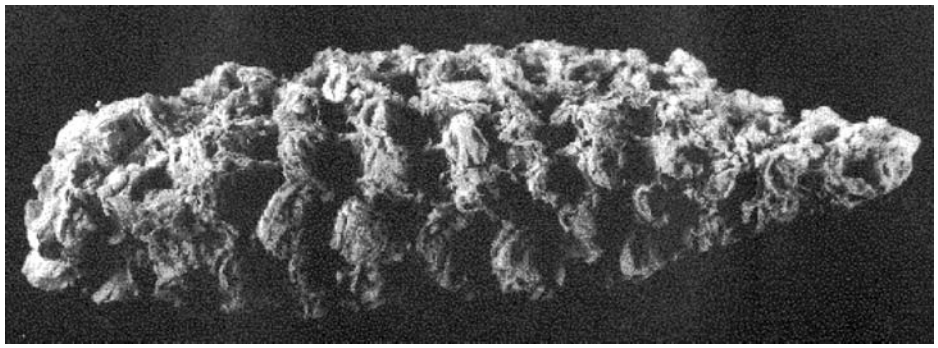
Centers of Domestication of Crop Plants



Gepts 2002, 2003

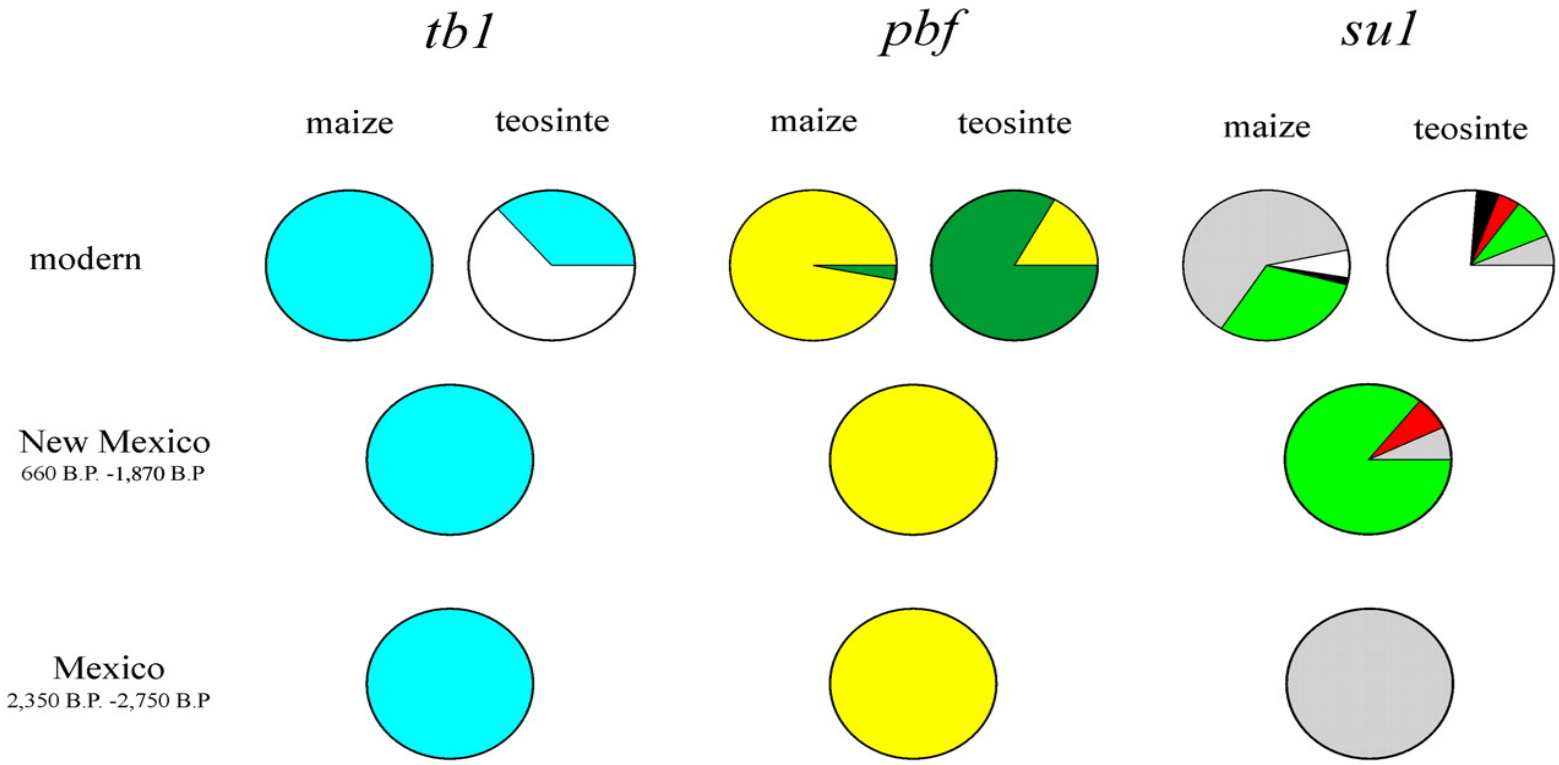
Major Findings about Domestication

- **Multiple, independent origins** of plant and animal agriculture in last 10,000 years
- **Genetic bottlenecks** in genetic diversity
- Important role of **genes with major phenotypic effect**
- Are genes for domestication **clustered?**
- **Molecular function** of genes for domestication
- Is there a **potential for domestication?**



Jaenicke-Després et al. 2003

Early allelic selection in maize as revealed by ancient DNA



Selection during domestication

- Selection intensity:
  - Wang et al. 1999: *tb-1* in maize
    - S = 0.04 – 0.08
  - Hillman and Davies: tough rachis in einkorn (1990)
- Time to fixation:
  - Wang et al. 1999:
    - Time to fixation: 315 to 1,000 years
  - Hillman and Davies:
    - Time to fixation: 20 to 200 years

Harvest	Relative fitness	
	Brittle	Tough
Beating - repeated	0.84	0.05
Beating - single	0.44	0.05
Sickle	0.40	1.00
Uprooting	0.43	1.00

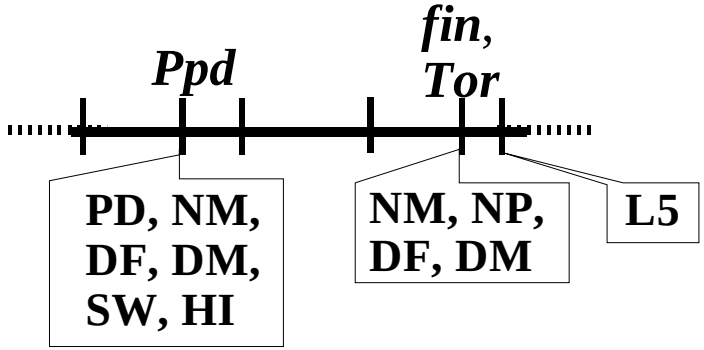
Major Findings about Domestication

- **Multiple, independent origins** of plant and animal agriculture in last 10,000 years
- **Genetic bottlenecks** in genetic diversity
- Important role of **genes with major phenotypic effect**
- Are genes for domestication **clustered?**
- **Molecular function** of genes for domestication
- Is there a **potential for domestication?**

Inheritance of the domestication syndrome in crops

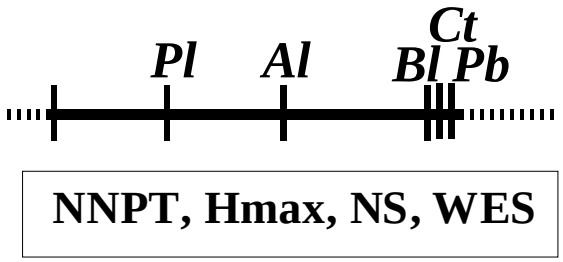
- Species studied:
  - Maize, common bean, rice, pearl millet, sunflower
- Common features:
  - Few loci
  - Major phenotypic effect
  - Most of phenotypic variation accounted for in genetic terms = high heritability
  - Few regions of the genome = linked
- Consequence:
  - Fast response to selection

Common bean, 2n = 2x = 22 (Koinange et al. 1996)



Growth habit, photoperiod sensitivity

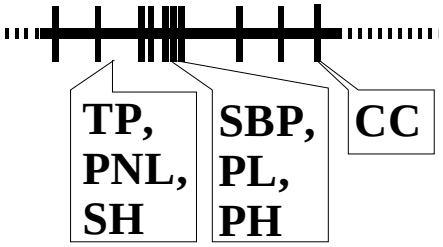
Pearl millet, 2n = 2x = 14 (Poncet et al. 2000)



Spikelet architecture and shedding, plant and spike morphologies and flowering

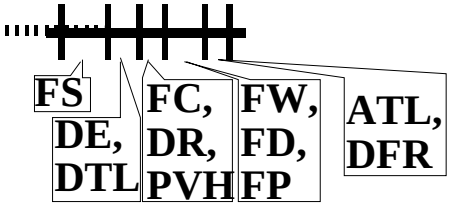
---

Rice, 2n = 2x = 24 (Xiong et al. 1999)

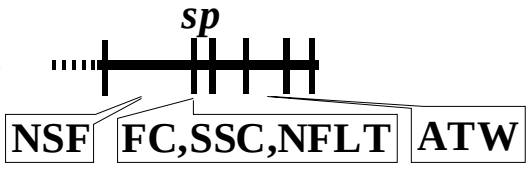


Plant and panicle morphology, shedding

Tomato, 2n = 2x = 24 (Grandillo and Tanksley 1996)



Fruit traits, earliness



Growth habit, fruit traits

Major Findings about Domestication

- **Multiple, independent origins** of plant and animal agriculture in last 10,000 years
- **Genetic bottlenecks** in genetic diversity
- Important role of **genes with major phenotypic effect**
- Are genes for domestication **clustered?**
- **Molecular function** of genes for domestication
- Is there a **potential for domestication?**

Cloning of Domestication Genes

Examples

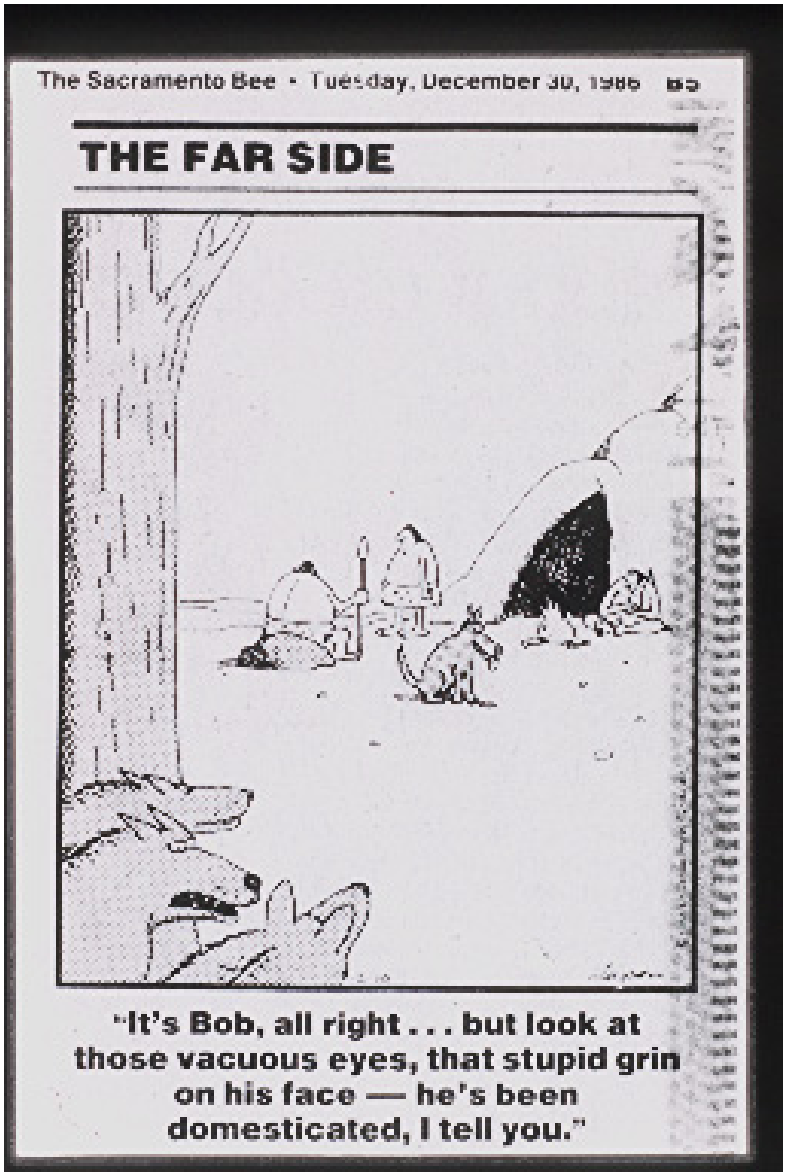
- *Tb-1* in maize: growth habit (Doebley et al 1997; Wang et al. 1999)
- *fw2.2* in tomato: fruit weight (Frary et al. 2000)
- *Hd1* in rice: flowering time (Yano et al. 2000)
- SHATTERPROOF in *Arabidopsis*: fruit dehiscence (Liljegren et al. 2000)

Major Findings about Domestication

- **Multiple, independent origins** of plant and animal agriculture in last 10,000 years
- **Genetic bottlenecks** in genetic diversity
- Important role of **genes with major phenotypic effect**
- Are genes for domestication **clustered?**
- **Molecular function** of genes for domestication
- Is there a **potential for domestication?**

Is There a Potential for Domestication?

- **Animals**
  - Docile (or selectable for docility); not afraid of humans
  - Non-territorial; tolerant to herding, i.e. not afraid of each other
  - Dominance hierarchy (Humans co-opt leadership role)
  - Uninhibited breeding
  - Rapid growth
- **Plants**
  - Some 250,000 angiosperm species
    - Less than 500 species domesticated
  - Trial and error domestication
    - Northern China, northeastern USA
    - Alfalfa domestication?
  - Inherent genetic potential?
    - Genetic variability
    - Morphological potential
    - Linkage of domestication genes
    - Probably not toxicity

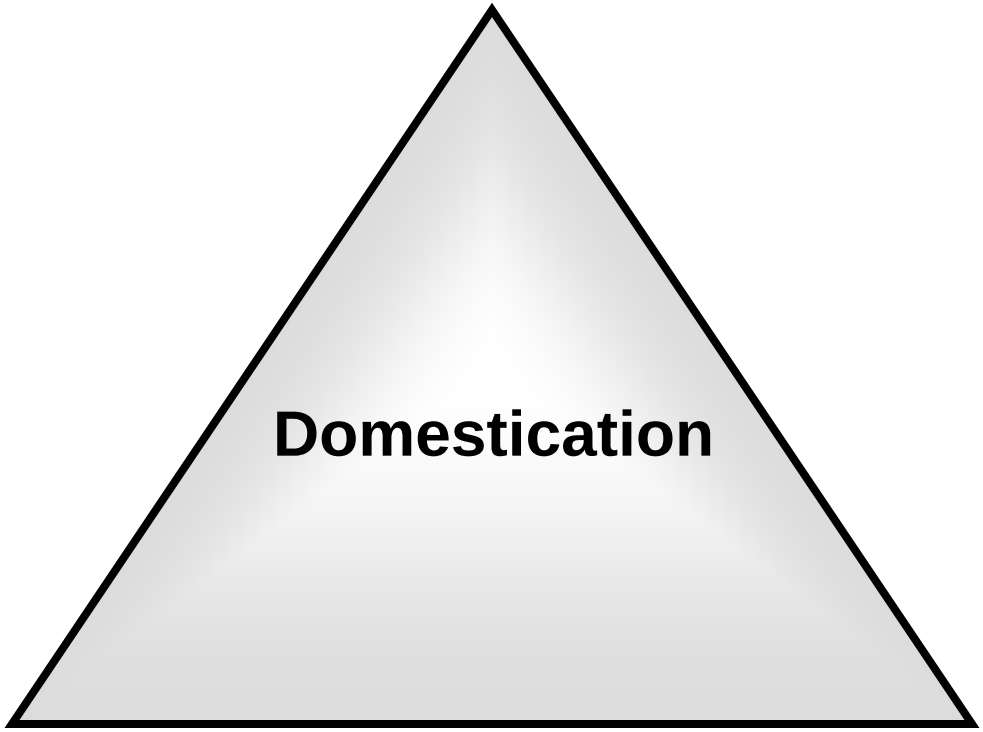


General characteristics of domestication

- **Selection** for adaptation to:
  - Growing or rearing condition
  - Utilization by humans
- **Heritable** changes as a consequence of bi-directional selection
- **Dependence** on humans for survival in thoroughly domesticated species
- **Mutually beneficial** relationship
- Necessary condition for the **development of civilizations**

Plant or Animal

Morphology
Behavior
Genetics



Humans

Cultural development:
knowledge of plants, animals
technology
Population growth

Environment

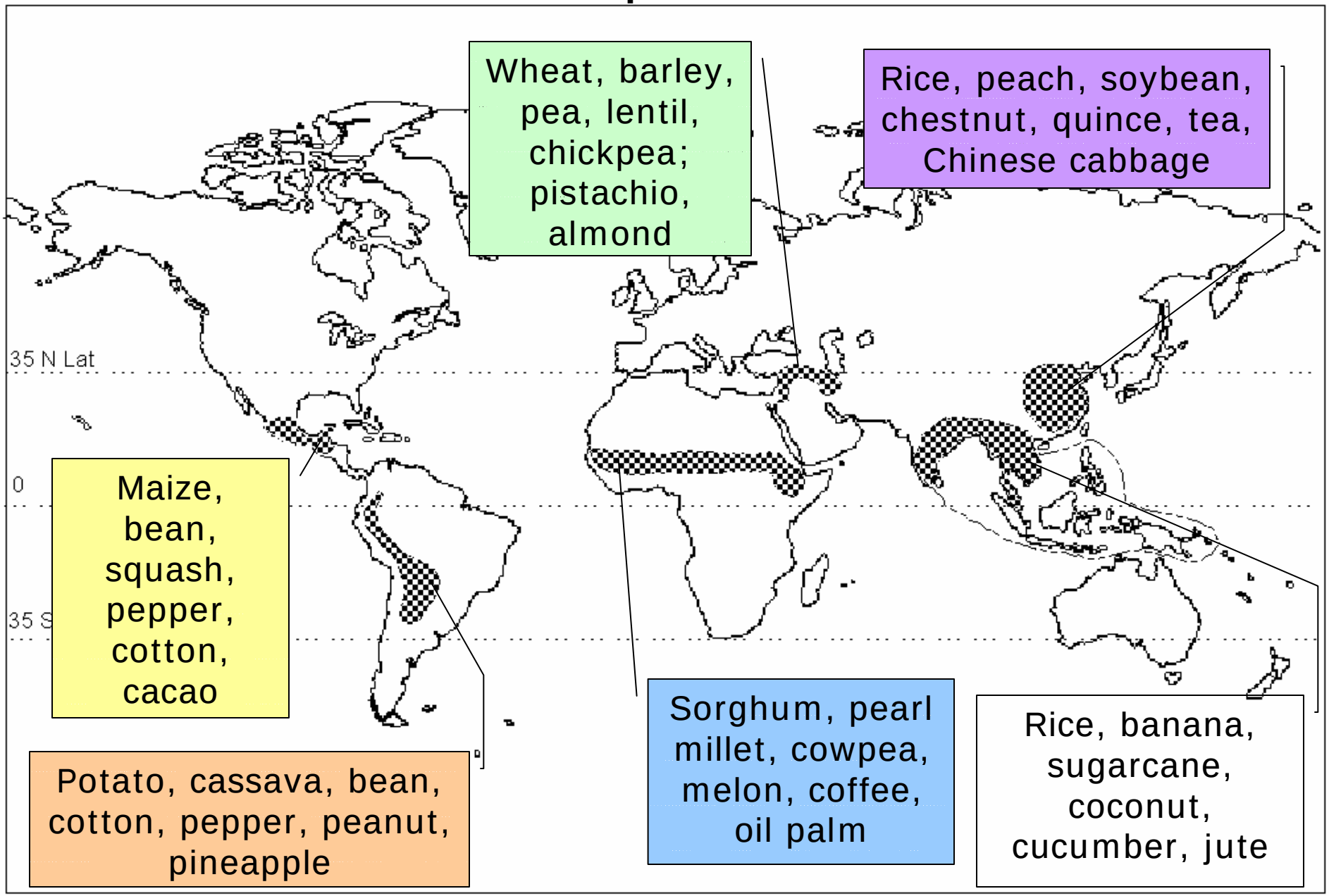
Climate change
Contrast between dry
and humid season
Diversity of niches

Gepts 2004

Applications to Agriculture

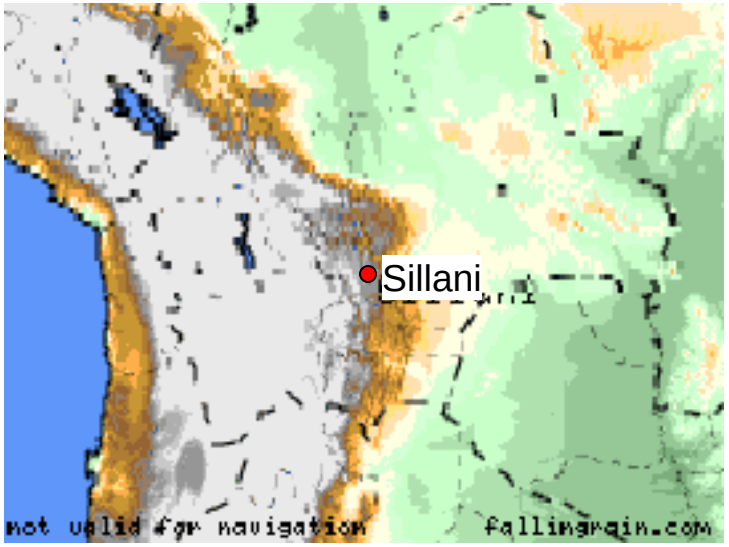
- **Where** to go for biodiversity?
- **What** plant material to use to broaden crop diversity?
- **Co-evolution** with pathogens and useful organisms

Centers of Domestication of Crop Plants



Gepts 2002, 2003

Nuña or kopuru (popping bean) growers

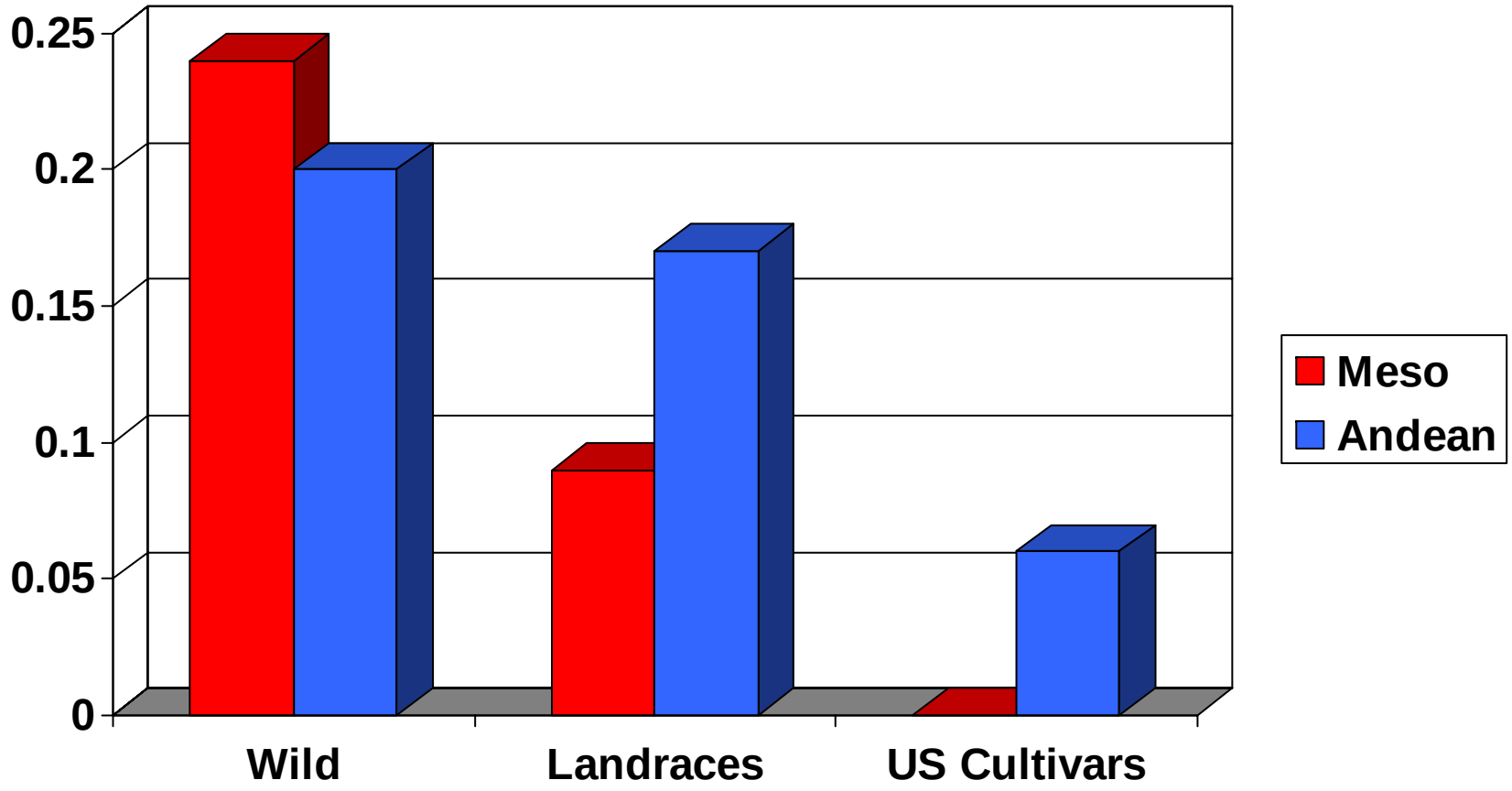


(Gepts 2004)

Applications to Agriculture

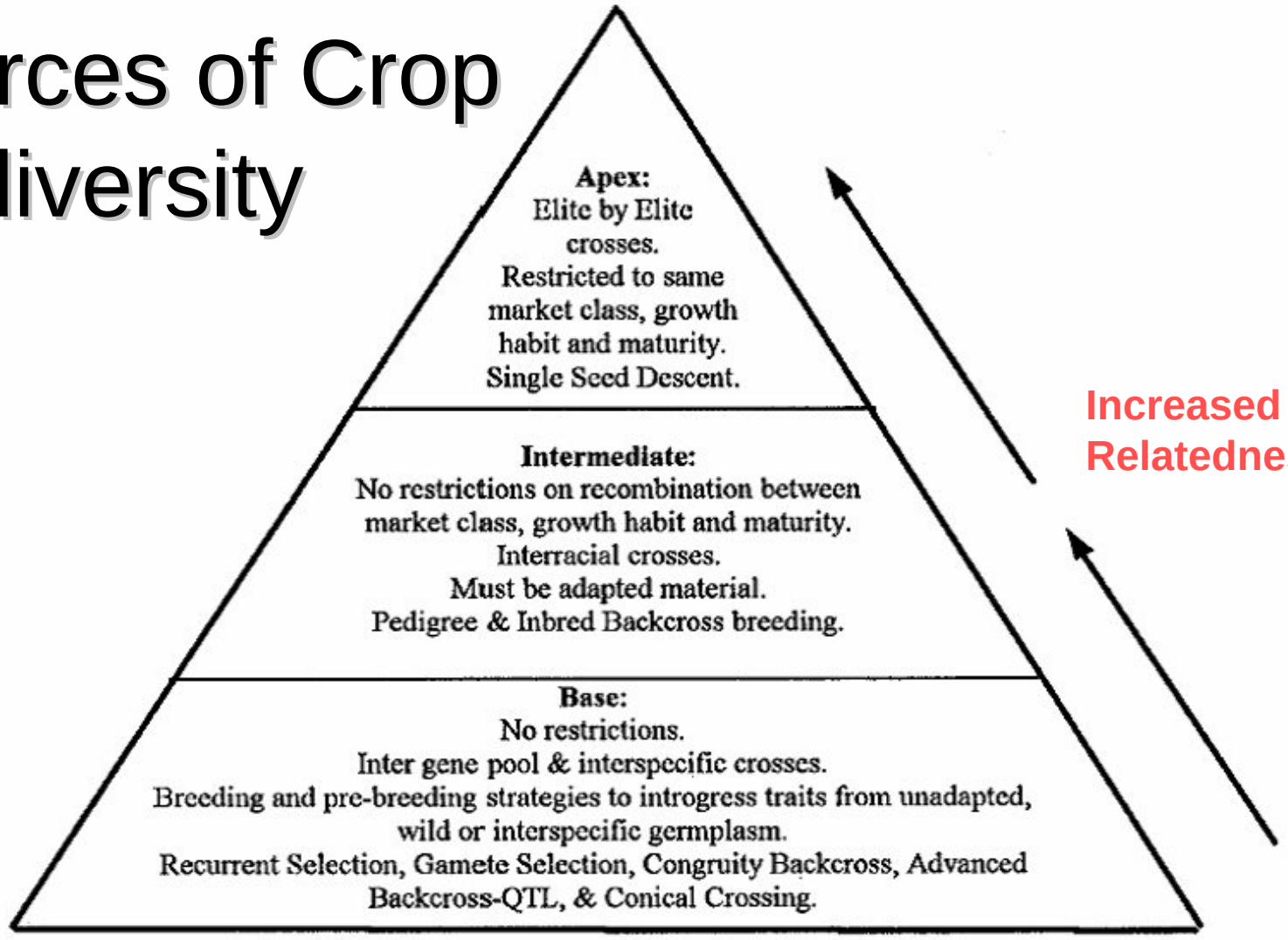
- **Where** to go for biodiversity?
- **What** plant material to use to broaden crop diversity?
- **Co-evolution** with pathogens and useful organisms

Reduction in Genetic Diversity in Common Bean during and after Domestication



Sonnante et al. 1994

Sources of Crop Biodiversity



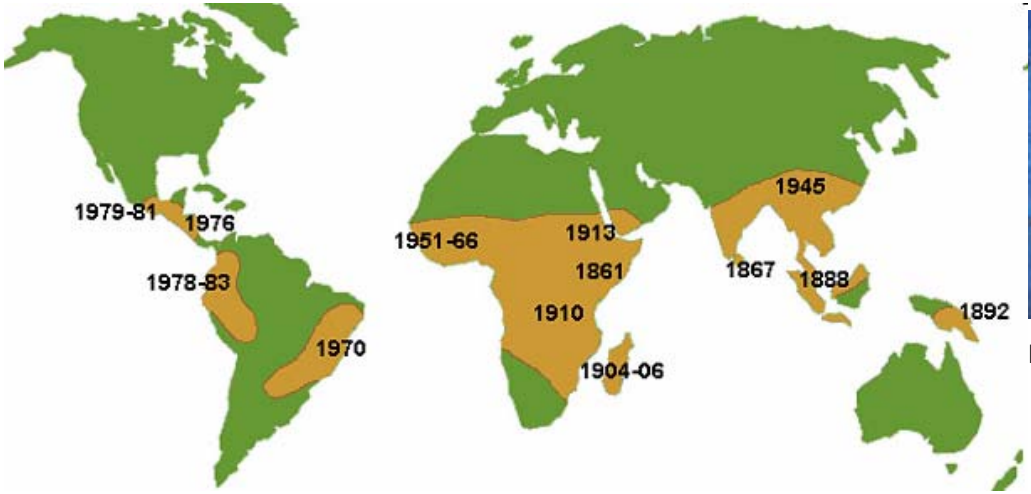
+ transgenes + genomic information

Kelly et al. 1998

Applications to Agriculture

- **Where** to go for biodiversity?
- **What** plant material to use to broaden crop diversity?
- **Co-evolution** with pathogens and useful organisms

Coffee Rust (*Hemileia vastatrix)*



From ARC-ITSC, South Africa

Potato late blight (*Phytophtora infestans*)

Corn Southern leaf Blight (*Bipolaris Maydis*)

(National Research Council (1972) Genetic vulnerability of crops. National Academy of Sciences, Washington, DC

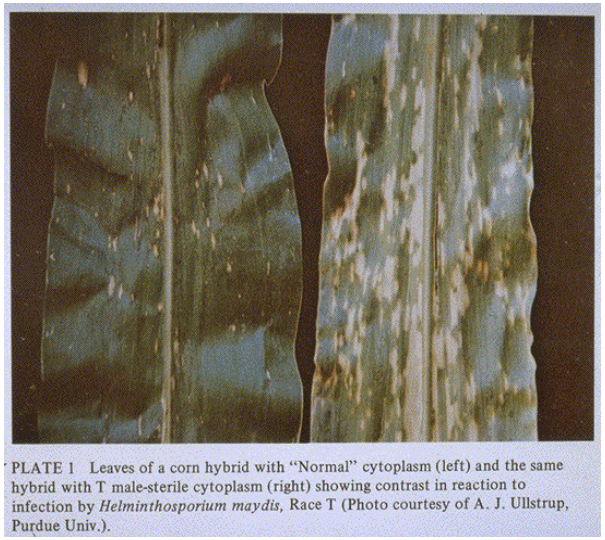


PLATE 1 Leaves of a corn hybrid with "Normal" cytoplasm (left) and the same hybrid with T male-sterile cytoplasm (right) showing contrast in reaction to infection by *Helminthosporium maydis*, Race T (Photo courtesy of A. J. Ullstrup, Purdue Univ.).

Conclusions

- Crop and domestic animal domestication:
  - Used by Darwin as an example of the potent effect of selection
  - Experimental model:
    - Known progenitor and descendants
    - Traits known
    - Time frame based on archaeological data
- Crop and animal breeding
  - Evolution in action
  - Measurable effect within lifetime (or PhD thesis!)

Sources

- General domestication:
  - Darwin, C. On the origin of species. http://www.esp.org/books/darwin/origin/facsimile/
  - Darwin, C. The variation of plants and animals under domestication. http://www.esp.org/books/darwin/variation/facsimile/title3.html
  - Diamond, J. 1997. Guns, germs, and steel Norton, New York.
  - Diamond, J. 2002. Evolution, consequences and future of plant and animal domestication. Nature 418:700-707 http://www.nature.com/cgi-taf/DynaPage.taf?file=/nature/journal/v418/n6898/full/nature01019_fs.html
  - Gepts, P. 2004. Domestication as a long-term selection experiment. Plant Breed. Rev. 24 (Part 2):1-44. http://www.agronomy.ucdavis.edu/gepts/LTS.pdf
  - History of food and agriculture: http://museum.agropolis.fr/english/pages/expos/fresque/la_fresque.htm
- Plant domestication:
  - Gepts, P. n.d. PLB143: The evolution of crop plants. Course notes. http://www.agronomy.ucdavis.edu/gepts/pb143/pb143.htm
- Animal domestication:
  - Price, E.O. Animal domestication and behavior. CABI, UK. Chapter 1: http://www.cabi-publishing.org/pdf/Books/0851995977/0851995977Ch1.pdf