The Agricultural Revolution:  
Plant Domestication and Breeding

http://www.wsu.edu/gened/learn-modules/top_agrev/agrev-index.html

The change from subsistence patterns (hunting and gathering) to agriculture was first ‘cultural revolution’, impacting human behavior, development of societies, and provided the economic basis of human ‘civilization’.
A 4,000 year ‘Revolution’

The shift to food production is related to *retreat of the ice age*, at the end of the Pleistocene era and beginning of the Holocene era.

The world became warmer and generally wetter beginning about 14,000 BC.

By 10,000 BC, climates were essentially modern. Parts of the Fertile Crescent became dried and could be cultivated.

The Agricultural Revolution took about *4,000 years to go from food foraging to complete dependence on domesticated products*. On evolutionary timeline, this was a sudden, rapid event.
Primary developmental stages were:

**Specialized foraging**
Beginning use of species that ultimately became domesticated

**Selection of desirable species**
Protection and weeding of naturally occurring plant communities

**Domestication of plants**
Gathering of seed, cultivation, plant selection, and associated genetic changes that lead to domestication.
Primary agricultural centers, timelines

Subtropical regions

Attributes: Geographically hilly and diverse topography; marked seasonality with cold, rainy winters and dry summers; host to large-seeded grasses and large flora of annual vegetation

Near east (i.e., the Fertile Crescent) beginning about 9,500 BC
Wheat and barley; Flax, lentils, figs, dates, grapes, olives, lettuce, onions, cucumbers, and melons; Fruit and nuts

http://www.nature.com/nrg/journal/v3/n6/slideshow/nrg817_F1.html
Meso-america – beginning about 7,200 BC
Maize, squash, common bean, lima bean, peppers, amaranth; Pollen records indicate domestication of maize by 5,000 B.C., sunflower by 3,000 B.C. in Central America. Evidence for Maize in Ohio by 280 B.C., in Virginia by 200 BC.

American societies at 500 BC resembled Mesopotamia at 5,000 BC. Likely due to lack of pre-adapted animals that could be domesticated and provide transport and traction needed for agrarian uses.

http://fga.freac.fsu.edu/maps.html
Other agricultural centers:

**Peruvian highlands** – beginning about 6,500 BC  
Tuber crops, potato, peanut, cotton, maize

**Far east (Thailand)** – beginning about 8,500 BC (less clear evidence)  
Rice, soybean, citrus fruits, coconut, taro, yams, banana, breadfruit, coconut, wet- and dry-land rice, sugarcane.

Many food crops are thought to have been spread from Indonesia to Melanesia and Polynesia. Earliest record of rice in Thailand is about 9,000 years B.C.

**China** - beginning about 7,800 BC.  
Major crops include millet and soybean
Consequences of domestication and monoculture

1. Dependency on few plants—

Agriculture made human communities, dependent on relatively few plants--the main crops which were grown--rather than on the many different kinds of plants which hunter-gatherers use. *Diets narrowed.*
2. Greater vulnerability to weather—

Dependency on fewer plants in turn makes agriculture a great gamble, as farming involves "betting" that the weather conditions will favor the growth of the particular crops planted.

Agriculture thus continues the ancient dependency of human life upon natural ecological systems, but it raises the odds of disaster in any given year.

3. Complete dependency on harvest times—

To survive, agriculturalists have to gather all their food for the year at one or two or three harvest times, rather than gathering year round. Nothing, therefore, can be allowed to interrupt the harvest. There is similarly a very narrow window of opportunity for planting and cultivating. Agriculturalists also have to store the produce of their fields for the rest of the year, protect it from moisture, vermin, and thieves.
4. Need for intense physical labor—

Agriculture requires intense and sustained physical effort—"drudgery"—at several times of the year, and on a scale previously unknown. In the Near East, cereal-growing required back-breaking labor at both sowing and harvest times. The labor of both men and women was required in the fields. As can readily be imagined, these conditions encouraged the development of social as well as individual discipline.

5. Population growth –

Mobile hunter-gatherer groups must necessarily limit the number of children. Sedentary agriculturalists, however, do not face such natural constraints. On the contrary, large families of many children mean more hands to help in the fields. After 10,000 years of this way of life, the human population is still expanding exponentially.
6. Pollution –

Advantages of sedentary life brought with them a set of new problems: for example, the problem of polluting one's living space. Nomads can stay clean and healthy simply by moving frequently. They do not need to develop elaborate cultural means of disposing of their dead, or of their food wastes or excrement, or of the wastes of their livestock.

7. Infectious disease –

Infectious disease is a problem closely related to population growth and to the difficulty of maintaining a clean, healthy living space. Clustering of both humans and animals together in unsanitary villages created a perfect environment for pathogens of all kinds.

Gradually, agriculturalists developed immunity to specific pathogens. The now common "childhood diseases" like mumps and measles and chicken pox are the relatively harmless descendants of once fatal diseases. This is evidence that the new way of life changed its human populations genetically.
8. Monoculture and soil depletion –

The growing of a single crop in a field by definition substitutes a biological **monoculture** for the complex ecological system that existed on the same ground previously.

One unintended effect is that the **nutrients in the soil necessary to the growing of this particular plant are depleted**. Over a relatively short period of time, growing a single crop can deplete even very rich soil. This was a problem which **rendered many early agricultural sites uninhabitable** after a time. It is still a very serious problem.

9. Pests and pathogens –

Human farmers are consciously altering the environment and "selecting for" the plants they need for food or fiber. Unwittingly, they are also "selecting for" **any organism that can live on the crop**: "vermin," insects, pathogens, and diseases, etc. Thus, paradoxically, by increasing their food supply, farmers **simultaneously increased threats to their food supply**.
Plant Domestication

Domestication is process by which early wild-type crops are sown from seed gathered from wild stands.

Key to domestication:

*Selective advantage to rare mutants alleles, which are necessary for survival in cultivation*; or those unnecessary for survival in wild.

*Cultivation causes selection pressure* – resulting in allele frequency changes, gradations within and between species, fixation of major genes, and improvement of quantitative traits.

‘Varieties’ were developed as ‘carrier of traits’ between growers / locations / cropping seasons
Early domestication and important plant traits
http://agronomy.ucdavis.edu/gepts/pb143/lec08/pb143l08.htm

*Loss of seed dispersal and seed dormancy traits are most important in the domestication process*
Elimination or reduction in seed dispersal mechanisms

**Non-shattering**
Varieties with seeds that are retained and only break off during the threshing process

**Free threshing**
Varieties where the seed easily separates from husk or glumes during threshing

**Non-brittle rachis** (ex: see photos)
The rachis, as central axis of a raceme or spike, should remain intact to facilitate threshing and minimize seed loss
Non-dehiscence

(The spontaneous opening at maturity of a plant fruit structure)

Example - left photo: Two genes in Arabidopsis have been identified that, when inactivated, prevent this weed from shattering its seed-containing pods.
Compact growth habit
Reduction in branching, height
Synchronous tillering
Synchronous flowering
Synchronous ripening

Climbing – to bush habit (i.e., Beans)
Reduction in internode length
Reduction in number of nodes, branches
Suppression of twining response
Determinacy (simultaneous flowering)

Common bean
Harvesting: Increases in seed yield

- Increase number of seeds
- Reduced sterility
- Larger inflorescence size
- Increased number of inflorescense

Pearl Millett - wild vs domesticated
http://agronomy.ucdavis.edu/gepts/pb143/lec08/pb143l08.htm

Reduction in daylength sensitivity.

Contributes to broader environmental adaptation in cultivated plants.

There is adaptive value of sensitivity in wild plants. Sensitivity provides mechanism to avoid non-optimal growing conditions.
Increased seedling vigor, improved emergence from planting

Larger seed
  More carbohydrates; increased reserves
  Fewer #, larger seeds

Non-dormant seeds
  Adaptive value of dormancy for wild type
  Conflict – premature germination
  Correlated response: reduced chaff

Reproductive system

Change from outcrossing to predominantly selfing for many crops

Reduced or absence of sexual reproduction
  Banana, plantain, navel orange

Vegetatively propagated – *instant domestication*

http://aggie-horticulture.tamu.edu/syllabi/201h/ediblebotany/index.html
Adaptation to taste and food utilization

Color, flavor, texture, storage quality, cooking quality, uniformity, etc.

Reduced toxic compounds

Cyanogenic glucoside: cassava and lima bean
Bitterness; phenolic compounds, etc., in wild seeds/plants

Processing and cooking quality:

Selection for ‘functional’ starch, protein and oil composition
Genetic control of domestication is relatively simple:

Relatively few genes and genomic regions involved

   ex: 1-2 genes control brittle rachis trait in wheat

Genes for domestication represent a only a small subset of unique genes/traits for that species

Several genes have major effect on plant phenotype

Once identified, domestication could occur quite rapidly

Genetic diversity available in the specie may not be carried through the domestication process
Plant breeding as a ‘science’

The rediscovery of Mendel’s laws in 1900

Hugo de Vries, Carl Correns, Erik Tschermak

In 1900, De Vries, a Dutch botanist, was ready to publish his experiments with the silene plant (Catchfly). In the process he found Mendel’s 1868 paper. Concurrently, Correns in Germany and Tschermak in Austria were also experimenting with plants and similarly ran across Mendel’s paper much to their surprise.

W. J. Spillman - 1901, Washington Agricultural College (WSU)

Spillman independently rediscovered Mendel’s Law of Heredity through experiments to hybrize wheat. Spillman has been credited with a major role in the acceptance of Mendel’s Law by scientists and agriculturalists in the United States.
Consequences of plant domestication and breeding

1. Crops are a combined product of artificial selection (man-directed) and natural selection

*Modern crop plants have been highly ‘genetically modified’ from their progenitor species due to man’s intervention and selection over thousands of years*

Teosinte

Maize
2. Modern crop plants were selected and bred for growing under cultivated conditions

Without cultivation, most crops are not able compete with weeds and pests and will not survive ‘in the wild’. Evolutionary traits and plant architecture important for competitiveness and survival have been lost or eliminated through breeding and selection.

In the last 100 years, selection has emphasized plant traits that facilitate mechanized planting, harvesting, and crop management. These traits are very unlikely to be advantageous to survival ‘in the wild’.
3. Most modern crops are relatively genetically uniform, leaving them highly vulnerable to changing races of diseases and insects.

Numerous ‘genetic bottlenecks’ have occurred in development of major crop species, from initial domestication through the release of modern high yielding varieties.

Conservation of genetic resources, especially land races and weedy progenitor species, is critical to maintain progress in plant improvement and reduce genetic vulnerability of modern crops to diseases and insects.
4. Modern plant breeding techniques have effectively expanded the germplasm base for many crops to include related species.

Most major wheat varieties are products of ‘chromosome engineering’; incorporating genes, chromosome segments, and chromosome translocations from different, but related species

Ex: Important gene introgressions (chromosome segments) from related weedy species transferred into wheat:

1B/1R and 1A/1R wheat - rye chromosome translocations

‘Hope’ gene for stem rust resistance from Agropyron

Numerous genes for resistance to leaf rust and Hessian fly from T. Tauschii
### Ex. Derivation of VPM resistance to Strawbreaker footrot

<table>
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<tr>
<th>Aegilops Ventricosa</th>
<th>T. Persicum</th>
<th>Ventricosa x Persicum</th>
<th>T. Aesticum 'Marne'</th>
<th>VPM</th>
<th>42 chr</th>
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<td>24 chr.</td>
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<td>42 chr.</td>
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<td>DM genome</td>
<td>AB genome</td>
<td>ABDM</td>
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Processes of Modern Plant Breeding

1. **Identify morphological, physiological and pathological traits** in a cultivated species that contributes to its adaption, health, productivity, suitability for end-use (food, fiber, industrial) products.

2. **Search out new germplasm and "new genes"** that encode for desired traits in different strains of the cultivated species, from different research programs, from closely related relatives, or in gene banks.

3. **Combine the germplasm and genes** for the desired trait(s) into an improved cultivar through traditional breeding and/or biotechnology.

4. **Assess the performance** of the "improved" breeding lines in the adapted environment(s) in comparison with current cultivars.

5. **Distribute the superior breeding materials** as a new cultivar to growers

*Plant breeders work as integral members of a team designed to improve the productivity of agriculture resulting in the release of improved cultivars to growers.*
Wheat Improvement and Breeding at OSU

Goal:
‘Deliver technology and profitability to Oregon growers through research, development, and release of improved wheat varieties’

Foundations:
Free exchange of germplasm and information

Extensive germplasm base established through worldwide collaborations and exchanges

Conventional field breeding program, with collaborative research into applications of molecular genetics and cereal chemistry techniques
Selection Priorities for Variety Development:

**Grain yield** - Yield stability, adaptation to environment and management

**Grain quality**
Test weight
Kernel size, weight

**Stress tolerance**
Optimal maturity
Winterhardiness
Drought and heat tol.

**Disease resistance**
Septoria
Mildew
**Stripe rust**
Cephalosporium stripe
Dryland footrots
**Strawbreaker footrot**

**End-use quality** -
Soft and hard wheat quality; 85% of Oregon wheat is exported
Yield (bu/a)

Frequency

Nursery Mean = 103.2
Selected Mean = 118.1
Stephens Mean = 113.0

Sites are chosen to represent the wide range of environments and management situations for wheat production in Oregon and to facilitate screening for disease resistance and stress tolerance.
End-use quality evaluation and research

‘Industry acceptability’ is required for variety release

Soft wheat quality – cookies, cakes

Hard wheat quality – bread, noodles
Products of OSU Wheat Breeding

Varieties are owned by OSU, openly released to the public for commercial production

Seed is available and sold to any interested seed company or farmer for propagation and production

Varieties are registered and protected under USDA Plant Variety Protection Act

Seed must be identified, sold under the variety name

There is no restriction on farmer-saved seed

PVP research exemption ensures that others can use the variety in breeding through crossing without restrictions on resulting progeny
As a product of conventional plant breeding, wheat varieties meet ‘GRAS’ criteria

‘GRAS’ - Generally Recognized as Safe’

There are no marketing or end-use restrictions.

Conventionally developed crop varieties do not require approvals from FDA, USDA, or EPA for release.

‘Tubbs’ SWW
Wheat Breeding Contributions and Impact:

R and D timeline: *10 to 12 years from cross to variety release.*

Life-span of a wheat variety: *average of 4 - 6 years*

Average cost of variety development: *$1+ million per variety*

Average yield increase per year from breeding: *0.5 to 1%*

Total yield increase from breeding since 1950: *2X to 3X* (depending on growing region)
New directions in public variety development:

Public-private partnerships to:
  Deliver products of biotechnology
  Market novel traits
  Identity-preserve, market value-added processing traits

Example: ‘ORCF-101’ is a CLEARFIELD* herbicide tolerant wheat variety released by OSU in 2003 for its utility in control of grassy weeds.

It was developed and released in collaboration with BASF Corporation, which has patent rights to the gene and technology.

ORCF-101 was released to seed industry through non-exclusive license to grow, promote, and sell seed. Growers are unable to save seed of CLEARFIELD* varieties and must purchase Certified seed each year.

CLEARFIELD* trait is not a product of GM technologies; it was developed via chemical mutagenesis.