CROP DOMESTICATION
Case Study: Barley (Hordeum vulgare)

Overview:
Domestication is the term commonly used to describe the evolution of species to a form suitable for agriculture. The domesticated crop evolves as a result of significant selective pressure by humans.

The appearance of domesticated crops correlates with the appearance of complex human societies. So, the idea of

"Seeds to Civilization"

is a common one: without agriculture, the complexities of civilisation could not have occurred.

It's worthwhile to step back and re-consider the concept of "Seeds to Civilisation".

Even up to fairly recent times, there were many human societies that did not engage in agriculture - commonly described as 'hunting/gathering' societies.

As Jack Harlan notes. (The Living Fields. our agricultural heritage. Cambridge University Press), it actually takes a lot of energy to engage in agriculture. He showed that hunting/gathering has a much higher efficiency (that is output/input is much higher), even working in the field, harvesting wild stands of emmer again, to show how easy it is.

Interviews with members of hunter/gatherer societies suggest they ~~may~~ judge agriculture to be a trouble.

"You depend on the sun and the rain just the same as we do but the difference is that we just have to go and collect the food when it is ripe; we don't have all this other trouble" (quotation from an Australian Aborigine informant. Harlan page 26)

~~Nothe~~ Note that hunter/gatherer societies often manipulated the landscape, often by burning, to create ecological conditions suitable for growth of stands of edible plants.

The very act of domestication brought with it the need for a much higher level of exertion, but the result could be (though not always) a higher yield.

The question that arises, then, is what is domestication? And, how was it discovered?

To explore what domestication is, I thought it might be appropriate to present the oldest written account of agricultural practice. A Farmers' Almanac from Sumer.

The almanac describes a sophisticated agronomic method, from ~ 4,000 years ago, that is really, in its essentials, how agriculture is done today.

The Farmers' Almanac details the following:

MAY-JUNE – ① Inundation of the fields. Oxen are introduced to trample the inundated soil as a way to remove weedy growth.

② Soil Preparation – Initially, smoothing the soil (breaking soil clods etc.), following by plowing.

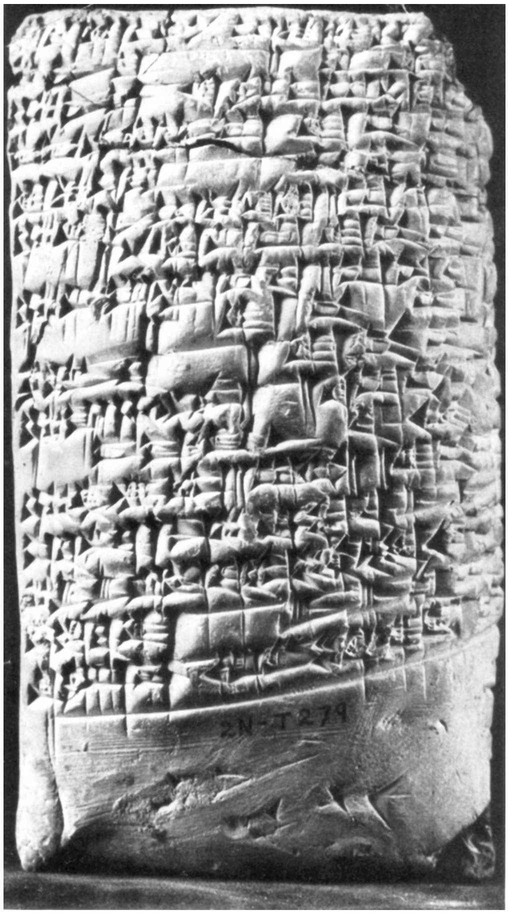
③ Seeding – A seed plow is used to ensure the seeds are planted at an appropriate depth and density.

④ Protecting the seeds from animals and birds (by prayer & by scaring them off).

⑤ After germination, irrigating

⑥ Nearing maturity, irrigate again.

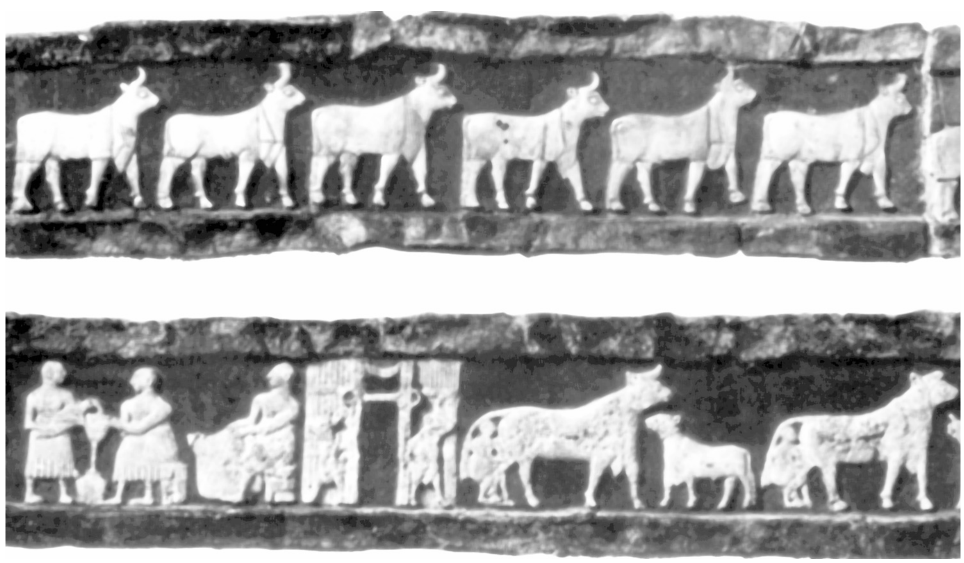
MAY-JUNE. ⑦ Harvest – the barley is mown and bundle together for drying. Then, it is threshed to break the seeds out of the inflorescence. Finally, it is winnowed to remove chaff.



Farmers’ Almanac. The reverse of the tablet which gives instructions for a yearly cycle of agrucultural activities. The cuneiform tablet dates back to about 3,700 years ago. The extant almanac is scattered amongst more than a dozen excavated tablets and fragments.

Kramer, Samuel Noah (1963) The Sumerians. Their history, culture and character. University of Chicago Press.

Evidence of Agriculture. From the temple of Al Ubaid, the bas relief shows a herd of cows and dairy activities, such as butter preparation and milking, indicative of sophisticated farming practices and the use of domesticated animals. The relief dates to about 4500 years ago.



Kramer, Samuel Noah (1963) The Sumerians. Their history, culture and character. University of Chicago Press.

Farmers' Almanac. In days of yore a farmer instructed his son (as follows):
When you are about to take hold of your fields (for cultivation), keep a sharp eye on the opening of the dikes, ditches and mounds (so that) when you flood the field the water will not rise too high in it. When you have emptied it of water, watch the field's water-soaked ground that it stay virile ground for you. Let shod oxen (that is, oxen whose hooves are protected in one way or another) trample it for you; (and) after having its weeds ripped out (by them) (and) the field made level ground, dress it evenly with narrow axes weighing (no more than) two-thirds of a pound each. (Following which) let the pickax wielder eradicate the ox hooves for you (and) smooth them out; have all crevices worked over with a drag, and have him go with the pickax all around the four edges of the field (lines 1–12).
While the field is drying, let your obedient (household) prepare your tools for you, make fast the yoke bar, hang up your new whips on nails, amd let the hanging handles of your old whips be mended by the artisans, Let the bronze .... your tools "heed your arm"; let the leather "headbinder," goad, "mouth-opener," (and) whip uphold you (in matters requiring discipline and control); let your bandu-basket crackle; (all this) will make a mighty income for you (lines 13–21).
When your field has been supplied with what is needed, keep a sharp eye on your work. After adding an extra ox to the plow-ox-when one is harnessed to another ox, their plow is larger that (an ordinary) plow–make them .... one bur; they will make for you a .... like a storm, so that three gur barley will be planted in that one bur. Sustenance is in a plow! (Thus) having had the field worked with the bardil-plow –(yes) the bardil-plow– (and then) having had it worked over with the shukin-plow, repeat (the process).

Irrigation in various forms implies a very sophisticated infra-structure to supply water to the fields

The removal of "weeds" to minimize competition for the crop seedlings is a crucial step that maximizes the yield.

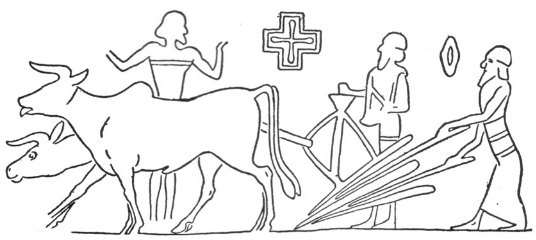
A gur is a measure of capacity, equal to about 120 liters. A bur is a measure of area, equal to about 63000 square meters.

Plowing exposes new soil, additional preparation creates a fine mix that optimizes seedling germination.

Kramer, Samuel Noah (1963) The Sumerians. Their history, culture and character. University of Chicago Press. The translation is tentative, with parentheses indicating additions by the translator, brackets partially illegible words, and lacunae (....) indicating gaps in the tablets/fragments. Line drawing of cuneiform tablet from Kramer, SN (1981) History Begins at Sumer. Thirty-nine firsts in man's recorded history. University of Pennsylvania Press.

(After) having had it (the field) harrowed (and) raked three times and pulverized fine with a hammer, let the handle of the whip uphold you; brook no idleness. Stand over them (the field laborers) during their work, (and) brook no interruptions. Do not [distract] your field workers. Since they must carry on by day (and by) heaven's stars for ten (days), their strength should be spent on the field, (and) they are not to dance attendance on you (lines 22–44). When you are about to plow your field, let your plow break up the stubble for you. Leave your "mouth-cover" of the plow ...., (and) leave your .... on a narrow nail. Let your moldboards spread to the side, set up your furrows –in one garush set up eight furrows. Furrows which have been deeply dug– their barley will grow long (lines 41–47).

When you are about to plow your field, keep your eye on the man who puts in the barley seed. Let him drop the grain uniformly two fingers deep (and) use up one shekel of barley for each garush. If the barley seed does not sink in properly, change your share, the "tongue of the plow." If the ...., (then) plow diagonal furrows where you have plowed straight furrows, (and) plow straight furrows where you have plowed diagonal furrows. Let your straight furrows make your borders into tulu-borders; let the lu-furrows make straight your borders; (and) plow ab-furrows where .... (Then) let all its clods be removed; all its high spots be made into furrows; (and) all its depressions be made into low furrows–(all this) will be good for the sprout. (lines 48–63).



After the sprout has broken through (the surface of) the ground, say a prayer to the goddess Ninkilim, (and) shoo away the flying birds. When the barley has filled the narrow bottom of the furrows, water the top seed. When the barley stands up as high as (the straw of) a mat in the middle of a boat, water it (a second time). Water (a third time) its royal barley. If the watered barley has turned red, what you say is: "It is sick with the samana-disease." But if it has succeeded in producing kernel-rich barley, water it (a fourth time), (and) it will yield you an extra measure of barley in every ten (lines 64–72).

The use of labor indicates sophisticated economics. Note the advice (not to dance attendance on you) which presumably means don't overwork your labor force.

In farming practice, ensuring the seeds are planted at the correct depth is crucial. Of all the steps in farming, ensuring maximal germination rates and seedling survival (both dependent on the depth of seed planting and seed density) are two factors which must be carefully controlled empirically. It's a science.

Irrigation during seedling growth and maturity are often carefully timed to maximize growth and yield.

Kramer, Samuel Noah (1963) The Sumerians. Their history, culture and character. University of Chicago Press. The translation is tentative, with parentheses indicating additions by the translator, brackets partially illegible words, and lacunae (....) indicating gaps in the tablets/fragments. Line drawing of a seedplow from Kramer, SN (1981) History Begins at Sumer. Thirty-nine firsts in man's recorded history. University of Pennsylvania Press.

When you are about to harvest your field, do not let the barley bend over on itself, (but) harvest it at the moment of its (full) strength. A reaper, a man who bundles the mown barley, and a man who [sets up the sheaves] before him–these three (as a team) shall do the harvesting for you. The gleaners must do no damage; they must not tear apart the sheaves. During your daily harvesting, as in "days of need", make the earth supply the sustenance of the young and the gleaners according to their number (that is, presumably, he must leave the fallen kernels on the ground for needy children and gleaners to pick), (and) let them sleep (in your field) as (in) the (open) marshland. (If you do so) your god will show everlasting favor. After you have obtained ...., do not ...., (but) roast (some of) the mown barley (so that) the "prayer of the mown barley" will be said for you daily (lines 73–86). When you are about to winnow the barley, let those who weigh your barley [prepare] for you (bins of) thirty gur. Have your threshing floor made level (and) the gur (-bins) put in order (ready for) the road. When your tools have been [readied] for you (and) your wagons put in order for you, have your wagons climb the (barley) mounds–your "mound-threshing" (is to take) five days. When you are about to "open the mound," bake arra-bread. When you open the barley, have the teeth of your threshing sledges fastened with leather and let bitumen cover the .... .When you are about to hitch the oxen (to the threshing sledge), let your men who "open" the barley stand by with (their–that is, the oxen's) food (lines 87–99). When you have heaped up the barley, say the "prayer of the (still) uncleaned barley." When you winnow the barley, pay attention to the men who lift the barley from the ground--two "barley-lifters" should lift it for you. On the day the barley is to be cleaned, have it laid on sticks, (and) say a prayer evening and night. (Then) have the barley "unloosed" (from the chaff) like (with) an overpowering wind, (and) the "unloosed" barley will be stored for you (lines 100–108).

These are the instructions of Ninurta, the son of Enlil. O Ninurta, trustworthy farmer of Enlil, your praise is good (lines 109–111)!

During the initial harvest, the seeds must not shatter (fall out of the ear), to maximize the eventual yield.

Kindness to children and the poor (who glean the fields) is common advice in many civilizations.

Threshing releases the seeds from the ear. Winnowing separates the seeds from the chaff.

Ears from two species of domesticated barley (Hordeum vulgaris, right, and Hordeum distichum, left) are shown. H. vulgare has six rows of seeds, H. distichum has two rows. Wild barley has two rows, with fewer seeds per ear and shatters easily.

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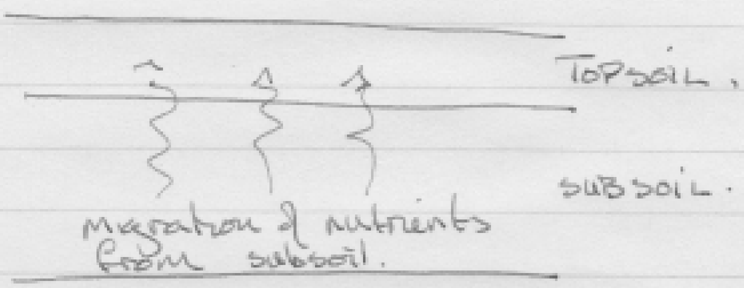
The major differences between Sumerian agricultural and modern are that slaves (?) have been replaced by machinery (plows, harrows and seed drills). And, even more important, most modern grain farming involves the application of fertilizer: comprised of essential macronutrients for the crop: Nitrogen, phosphorus & potassium.

This last innovation is very important, since it supports far more intensive agricultural practice.

In the past, crop fields have been taken out of production (fallowed) to allow ~~soil~~ nutrients in the top soil to replenish.



The depletion of soil nutrients has been a serious issue - effecting deteriorating crop yields over time.

An additional long-term problem is increases in salinity (NaCl) over time, especially in dry conditions where irrigation is used.
Salinization is can be a very severe problem.

Now that the complexity of "civilized" agricultural practice is understood, what is it about the crop species that makes it a domesticated rather than a wild species?

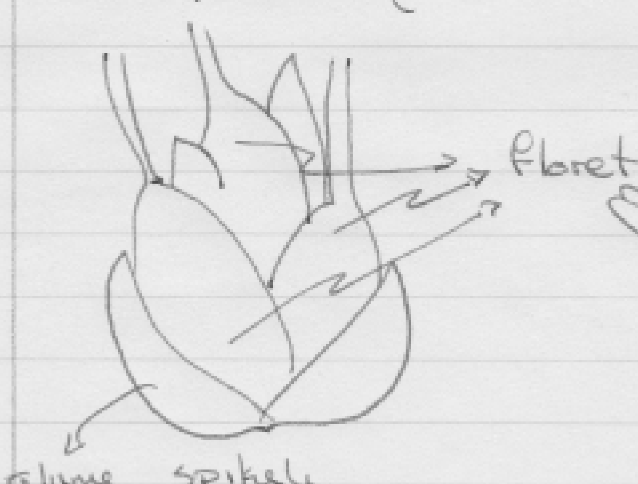
There are a number of traits that appear as a consequence of domestication. To explore them we need to understand the life cycle of the species.

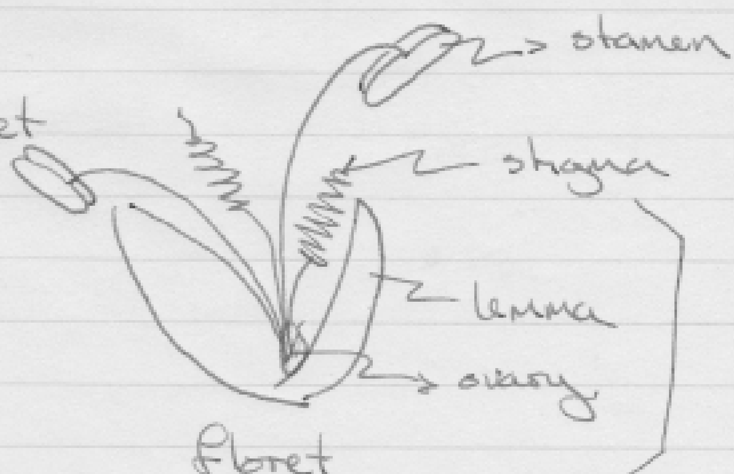
Barley is our case study. It is a member of the Grass Family (Gramineae).

Gramineae is a family in the Monocotyledonae

They are usually annual or perennial herbs (though some are woody - for example, the bamboos)

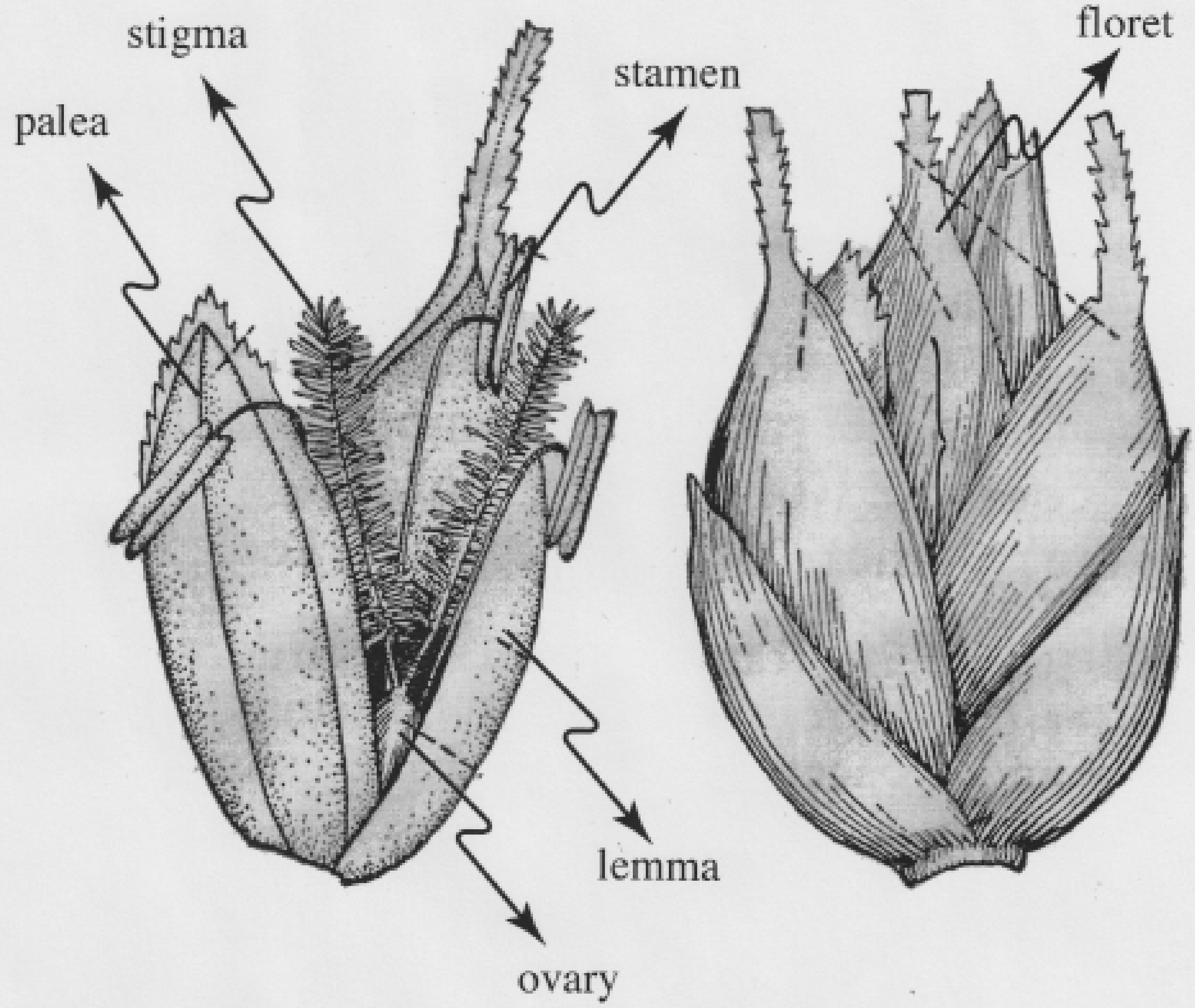
The floral arrangement is quite unique. The basic unit of the inflorescence is the spikelet. Multiple spikelets form the inflorescence. The spikelet itself is comprised of 1 or more florets.





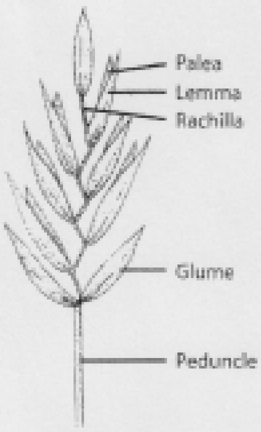
The stigmas are feathery - indicative of the wind pollination so common in the Gramineae.

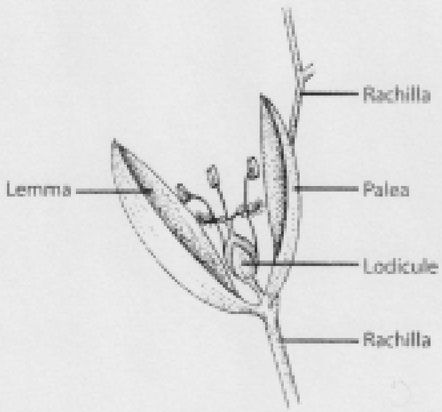
Grass Flower Anatomy

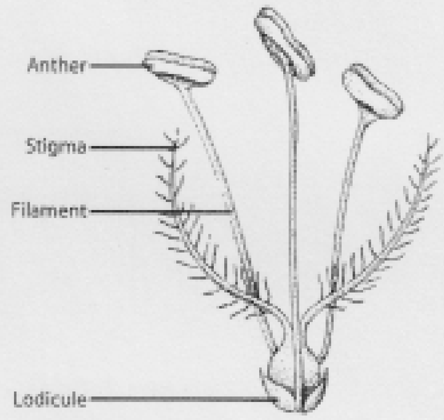


Grass floret (left) and spikelet (right).

Grass Flower Anatomy







Grass flowers usually develop in clusters (left). As a cluster matures, a single pair of dry, chaffy bracts –the glumes– separate a little, exposing the elongating spikelet, with from one to many florets (depending on the species of grass) attached to a central axis, or rachilla. Each floret is surrounded by two distinct bracts of its own, the palea and lemma (center). These are forced apart, exposing the inner parts of the flower, by the swelling of the lodicules –small, rounded bodies at the base of the carpel– and are spread wide when the grass is in flower (right). The stamens, usually three in number, have slender fiilaments and long anthers, and the stigmas are typically long and feathery and so are efficient at intercepting the wond-borne pollen.

The barley (and other) grasses typically have a fibrous root system from which the flag leaf and axillary leaves grow up.

The primary leaf ~~and~~ grows up first, followed by ~~&~~ the auxillary leaves: A process called tillering.

In wild species the timing of inflorescence formation is not synchronized. That is, tillers mature later.

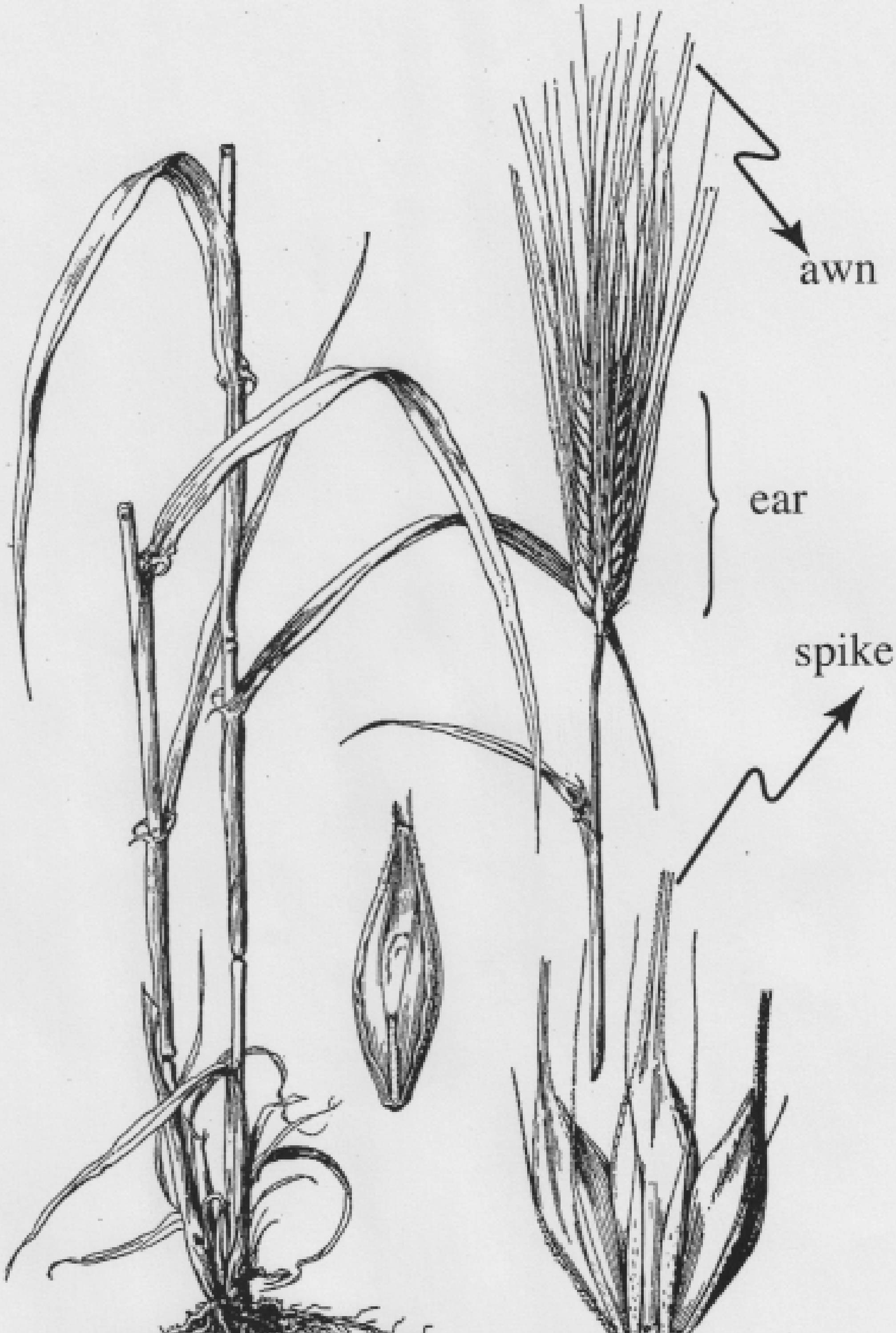
In domesticated species, all inflorescences mature at the same time.

Upon maturity of the inflorescence, pollination occurs due to wind. In some grasses, out-crossing is assured because the anther dehiscement and stigma maturity occurred at separate times. In Hordeum vulgare, selfing is common.

Once the seed is mature, the wild species has a number of traits conducive to dissemination and "planting".

The <u>awns</u> may attach to animals passing by, and may enhance wind-caused dissemination.

The <u>spikes</u> are often barbed. When the seed falls to the ground, the spikes assist in "drilling" the seed <u>into</u> the ground.



Barley. The awns function in dissemination of the seeds, latching onto passing animals. The spikes function in self-seeding. They penetrate the ground, and twist as the relative humidity changes to 'drill' the seed into the ground.

In domesticated barley, the awns and spikes are less developed than in wild barley.

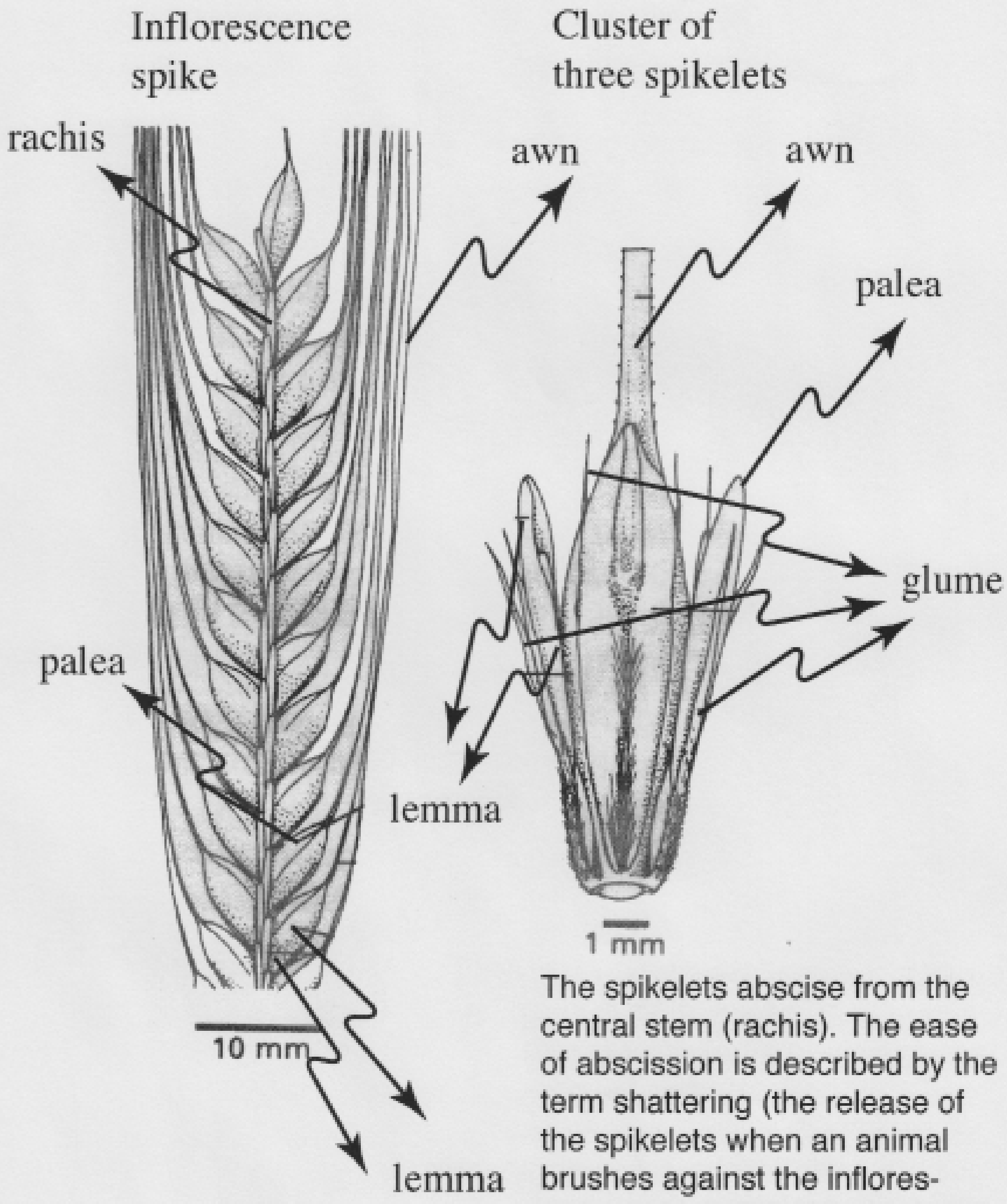
Of greater significance is the ability of the inflorescence to break apart into the individual ~~sk~~ spikelets. This is known as "shattering".

The spikets are arranged on a central structure called the rachis.

An abscission layer forms between the spikelet and the rachis, allowing it to break off easily.

While this may aid dissemination in the wild species, it will affect harvesting yield. Thus, an absence of shattering is a well-defined trait of domesticated barley (and other domesticated grasses).

Hordeum vulgare var. *distichum*.



The spikelets abscise from the central stem (rachis). The ease of abscission is described by the term shattering (the release of the spikelets when an animal brushes against the inflorescence, or wind carries the spikelets away). Domesticated barleys do not shatter, maximizing harvested yield.

One final trait is observed in domesticated barley: An increase in seeds within the inflorescence.

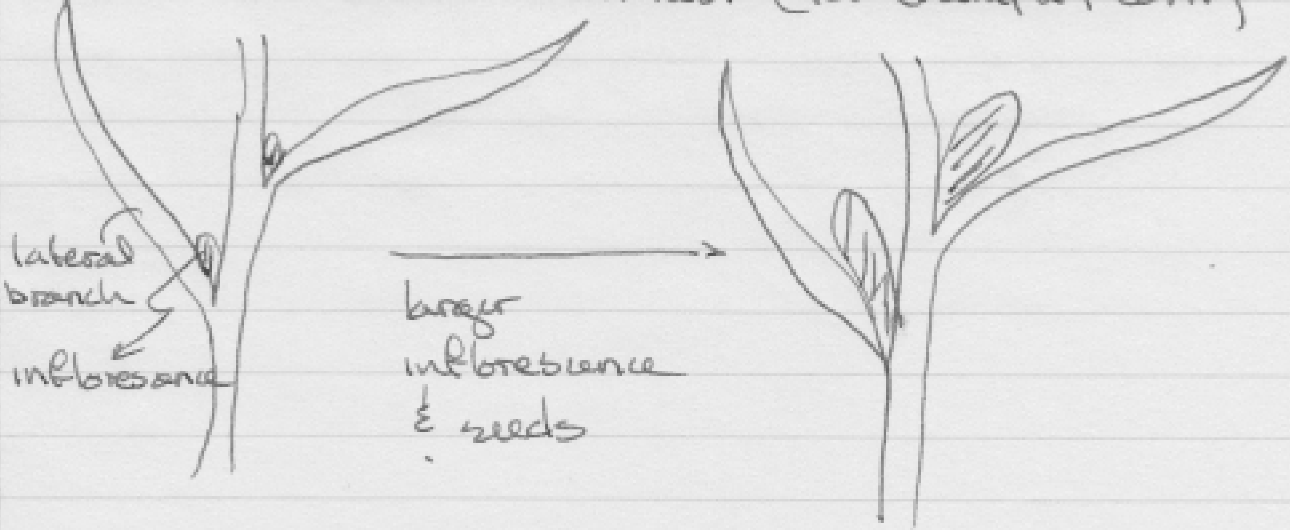
For all of these ~~Unlike the other~~ traits (~~especially shattering, but~~ (in general the inhibition of natural mechanisms of dissemination), increased seed yield would not have arisen as an unexpected outcome of harvesting by humans - but probably involved selection of seeds for planting in the next growing season.

These "adaptive syndromes" have been categorized by Jack R. Harlan (Crops and Man). Specifically, the selective pressures associated with harvesting (and planting of harvested seed) result in:

(A) Increase in percent seed recovered, due to.

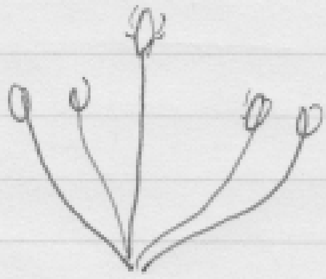
(1) ◦ Non-shattering.
(2) ◦ Changes in determinant growth habit.

(2a) for cereals which have their seeds borne on lateral branches. (for example, corn)



2b

for cereals that have unbranched culms (instead, they use tillering).



synchronous tillering and inflorescence maturation.

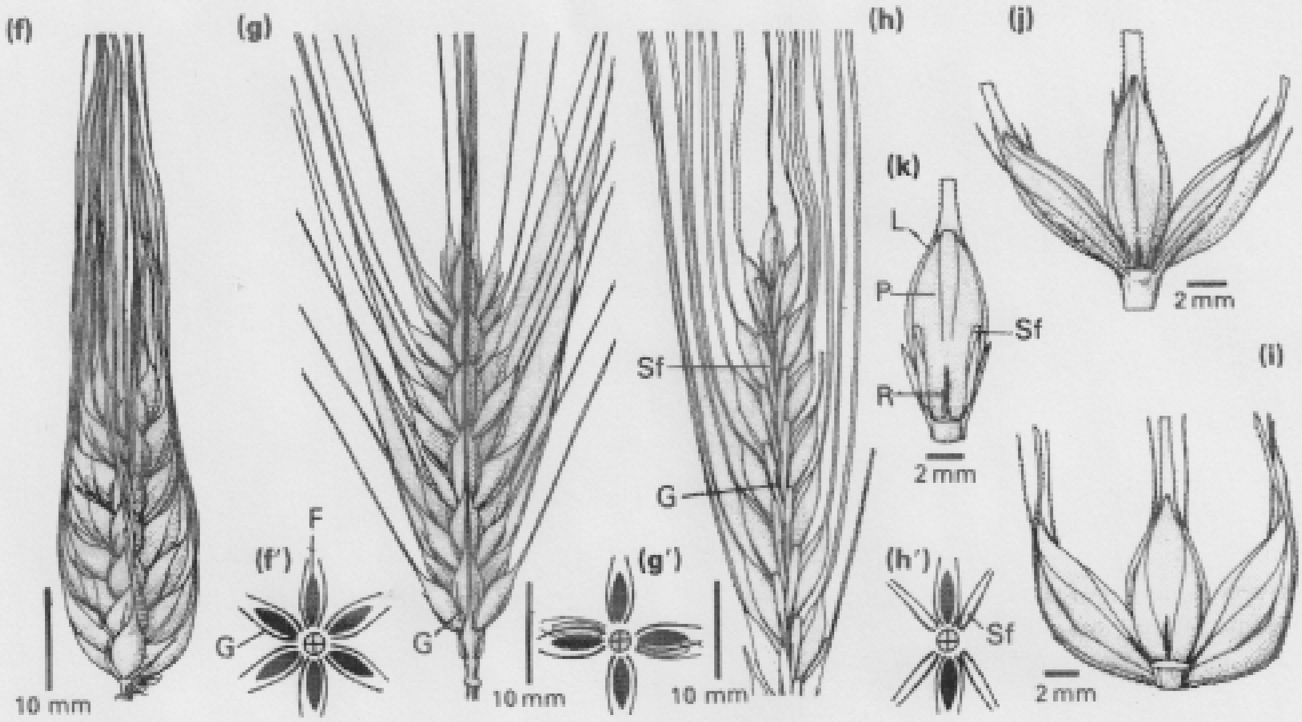
(B) Increase in seed production

1. Increase in percent seed set (that is, fertility)
2. steril florets become fertile.
   (distichum → hexastichum in the case of barley)
3. Increase in inflorescence size and/or number of inflorescences.

Additional selective pressures arise from the radically different environment of a cultivated field compared to the wild habitat. In the "mono-species" cultivated field, competition between seedlings created selective pressure that results in larger seeds with more food reserves - to maximize vigorous growth of the newly germinated seedling.

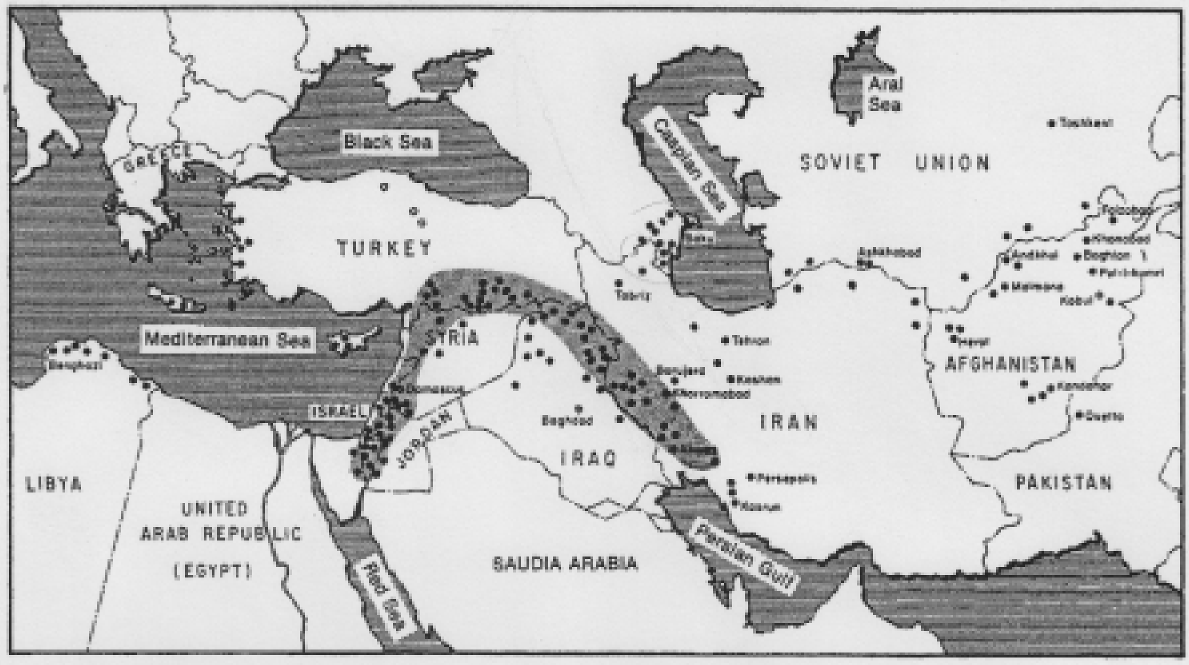
Dormancy mechanisms will be inhibited to ensure fast germination after planting.

Hordeum vulgare (Barley)



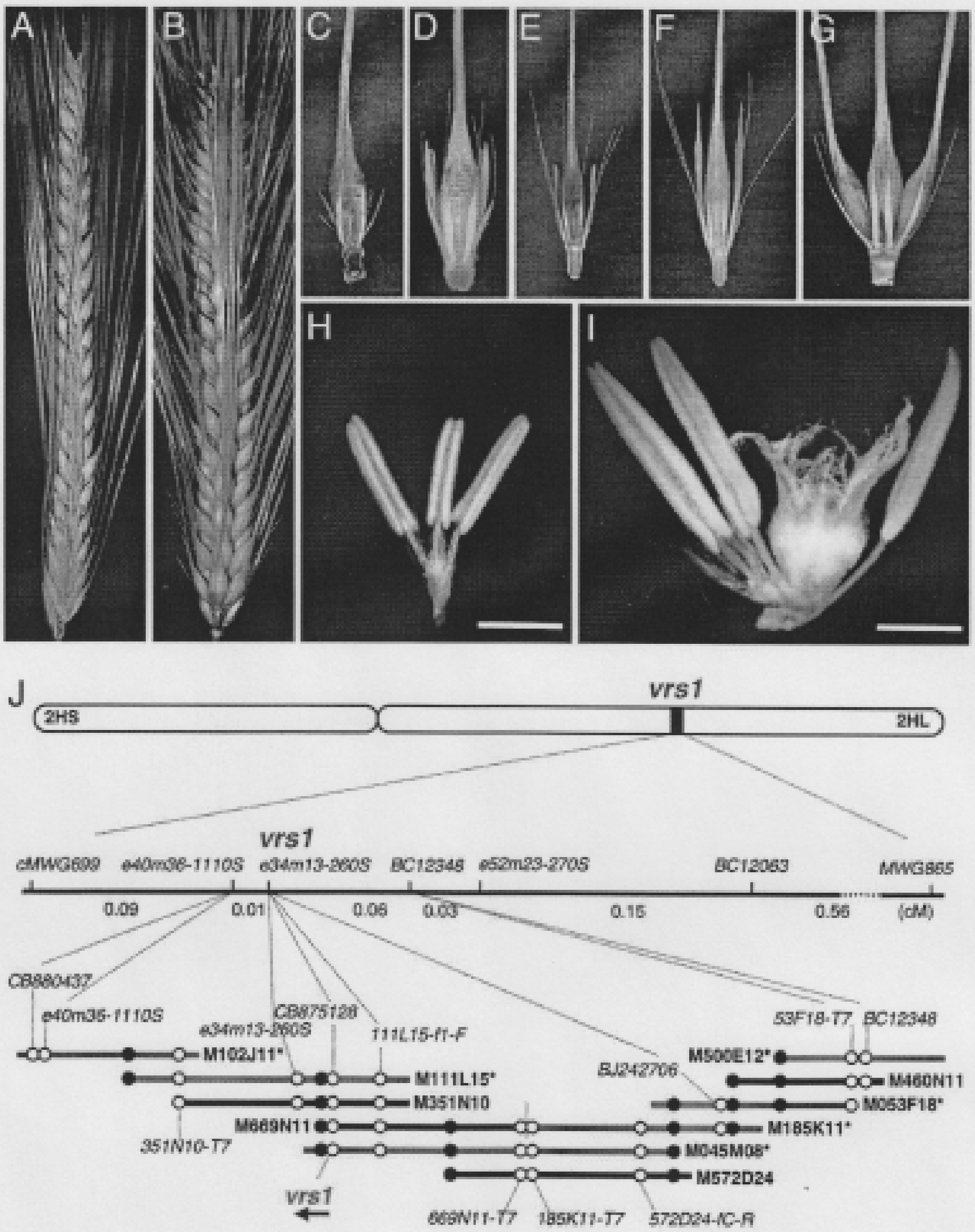
(f) var. *hexastichum* (g) var. *tetrastichum* (h) var. *distichum*

(f'), (g') and (h') spikelet layouts. (i), (j) and (k) clusters of three spikelets. F: floret; G: glume; L: lemma; P: palea; Sf: sterile floret.



Distribution of wild barley sites.

In the shaded area, massive stands of wild barley exist. Elsewhere, wild barley may be abundant, but normally confined to highly disturbed sites. The Russian botanist N.I. Vavilov proposed that the origin of a domesticated crop (such as barley) would correlate with the region of highest genetic variability, and collected many wild stocks as part of an exploration of genetic diversity. The concept has not been borne out by experimental evidence. In the example of barley, there is archaeological support for its first domestication in the "fertile crescent" (co-localizing with the shaded region above), but high genetic variability exists outside of this region. Thus, Ethiopian barley cultivars are known for resistance to leaf diseases, Tibetan barley cultivars have a gene for 'naked seeds' in high frequency. Other unique characteristics are found in East Asian barley cultivars. Source: Harlan JR (1992) Crops and Man.



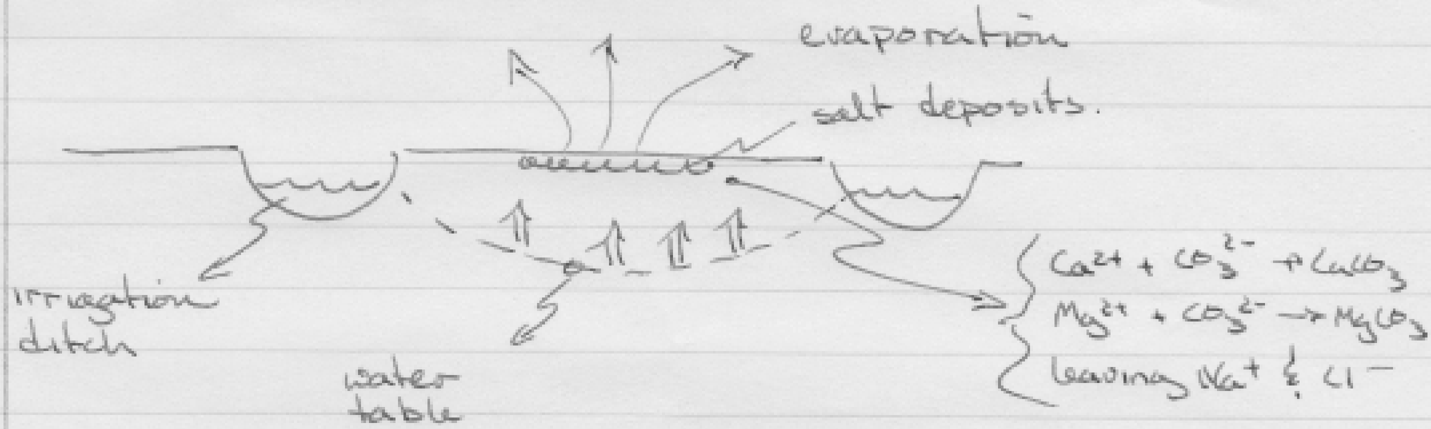
Map-based cloning of barley six-rowed spike gene vrs1. (A) Two-rowed spike. (B) Six-rowed spike. (C–G) One central and two lateral spikelets at a rachis node. (C) Ethiopian landrace var. deficiens; rudimentary lateral spikelets (Vrs1.t). (D) Two-rowed cultivar var. distichon; sterile lateral spikelets (Vrs1.b). (E) Wild barley var. spontaneum; sterile lateral spikelets (Vrs1.b). (F) Wild barley var. proskowetzii; short-awned or tip-pointed lateral spikelets (Vrs1.p). (G) Six-rowed cultivar convar. vulgare; fully fertile and awned lateral spikelets (vrs1.a). (H and I) Staminate floret of lateral spikelet (H) and hermaphroditic floret (I) in central spikelet in Vrs1.b two-rowed cultivar (D). (Scale bars: 2 mm.) (J) High-resolution linkage map and physical map.

Source: Komatsuda et al. (2007) Six-rowed barley originated from a mutation in a homeodomain-leucine zipper I-class homeobox gene. Proc. Natl. Acad Sci *USA* 104:1424–1429.

After Domestication: SOIL SALINIZATION.

In the absence of sufficient drainage and especially in arid regions (with rainfall less than 20 inches per year), salinization becomes a concern.

Under irrigation, the water table rises and brings with it dissolved salts. The water evaporates, pulling water (& the salts) up to the surface.



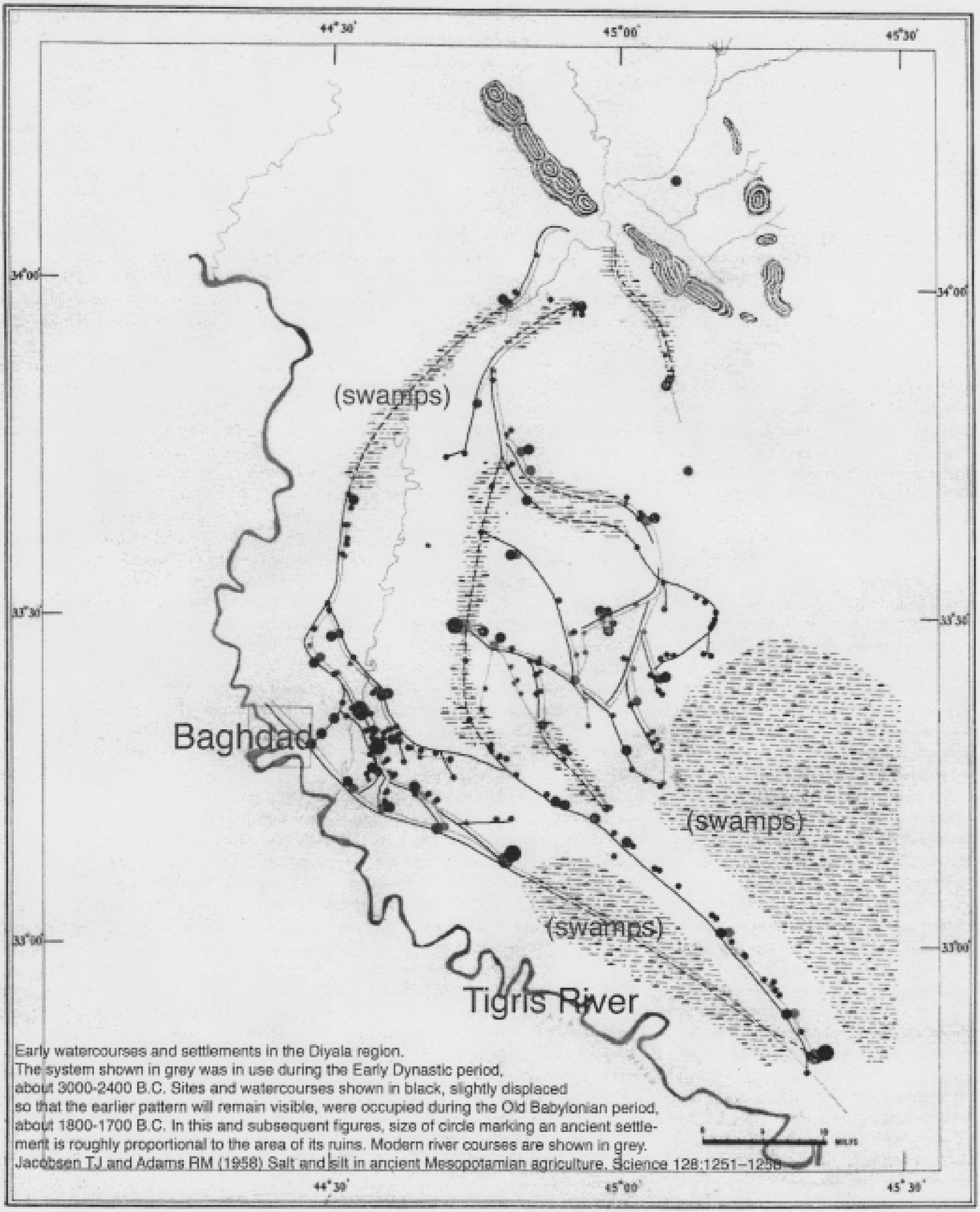
The nature of the salts can vary. chloride and sulfate salts of calcium, magnesium and sodium are common. If these accumulate in the topsoil (and especially NaCl * NEXT PAGE), the impact on agricultural yield is severe.

In the case of domesticated crops in Sumer, there is a historical record that suggests a shift from wheat (a halo-sensitive) to barley (a halo-tolerant) from ca 3500 BCE to 2500 BCE with a concomitant decline in yields from ca 2500 liters/hectare to 1500 liters/hectare within about the same time frame.
(Jacobsen & Adam 1958 Salt and silt in ancient Mesopotamian agriculture. Science 128 1251-1258.)

An additional challenge: silt deposition over time would have had an aggravating effect.

(*) In salinization, Ca^{2+} & Mg^{2+} typically precipitate as carbonate salts, leaving sodium to dominate the soil solution.

It is believed that this salinization was a major cause for a shift in towns & cities, which declined in the south. That is, the deep depreciation of soil resources was the cause of the downfall of a civilization.



Early watercourses and settlements in the Diyala region.
The system shown in grey was in use during the Early Dynastic period, about 3000-2400 B.C. Sites and watercourses shown in black, slightly displaced so that the earlier pattern will remain visible, were occupied during the Old Babylonian period, about 1800-1700 B.C. In this and subsequent figures, size of circle marking an ancient settlement is roughly proportional to the area of its ruins. Modern river courses are shown in grey.
Jacobsen TJ and Adams RM (1958) Salt and silt in ancient Mesopotamian agriculture. Science 128:1251–1258

21 November 1958, Volume 128, Number 3334 SCIENCE

Salt and Silt in Ancient Mesopotamian Agriculture

Progressive changes in soil salinity and sedimentation contributed to the breakup of past civilizations.

Thorkild Jacobsen and Robert M. Adams

Under the terms of a farsighted statute, 70 percent of the oil revenues of the Iraqi Government are set aside for a program of capital investment which is transforming many aspects of the country's predominantly agricultural economy. As compared with the subsistence agriculture which largely has characterized Iraq's rural scene in the past, new irrigation projects in formerly uninhabited deserts are pioneering a rapid increase in land and labor productivity through crop rotation, summer cultivation in addition to the traditional winter-grown cereals, and emphasis on cash crops and livestock.

But these and similar innovations often have disconcerting effects in a semiarid, subtropical zone—effects which cannot be calculated directly from the results of experiment in Europe and America. At the same time, old canal banks and thickly scattered ruins of former settlements testify to former periods of successful cultivation in most of the desert areas now being reopened. The cultural pre-eminence of the alluvial plains of central and southern Iraq through much of their recorded history provides still further evidence of the effectiveness of the traditional agricultural regime in spite of its prevailing reliance on a simple system of fallow in alternate years. Accordingly, the entire 6000-year record of irrigation agriculture in the Tigris-Euphrates flood plain furnishes an indispensable background for formulating plans for future development.

At least the beginnings of a comprehensive assessment of ancient agriculture recently were undertaken on behalf of the Government of Iraq Development Board. In addition to utilizing ancient textual sources from many parts of Iraq which today are widely scattered in the world's libraries and museums, this undertaking included a program of archeological field work designed to elucidate the history of irrigation and settlement of a portion of the flood plain that is watered by a Tigris tributary, the Diyala River (*1*). Here we cannot report all the diverse findings of the project and its many specialists, but instead will outline some aspects of the general ecological situation encountered by agriculturalists in the Mesopotamian alluvium which seem to have shaped the development of irrigation farming. And, conversely, we hope to show that various features of the natural environment in turn were decisively modified by the long-run effects of human agencies.

Historical Role of Soil Salinization

A problem which recently has come to loom large in Iraqi reclamation planning is the problem of salinity. The semiarid climate and generally low permeability of the soils of central and southern Iraq expose the soils to dangerous accumulations of salt and exchangeable sodium, which are harmful to crops and soil texture and which can eventually force the farmer off his land.

For the most part, the salts in the alluvial soils are presumed to have been carried in by river and irrigation water from the sedimentary rocks of the northern mountains. In addition, smaller quantities may have been left by ancient marine transgressions or borne in by winds from the Persian Gulf. Beside the dominant calcium and magnesium cations, the irrigation water also contains some sodium. As the water evaporates and transpires it is assumed that the calcium and magnesium tend to precipitate as carbonates, leaving the sodium ions dominant in the soil solution. Unless they are washed down into the water table, the sodium ions tend to be adsorbed by colloidal clay particles, deflocculating them and leaving the resultant structureless soil almost impermeable to water. In general, high salt concentrations obstruct germination and impede the absorption of water and nutrients by plants.

Salts accumulate steadily in the water table, which has only very limited lateral movement to carry them away. Hence the ground water everywhere has become extremely saline, and this probably constitutes the immediate source of the salts in Iraq's saline soils. New waters added as excessive irrigation, rains, or floods can raise the level of the water table very considerably under the prevailing conditions of inadequate drainage. With a further capillary rise when the soil is wet, the dissolved salts and exchangeable sodium are brought into the root zone or even to the surface.

While this problem has received scientific study in Iraq only in very recent years, investigation by the Diyala Basin Archeological Project of a considerable number and variety of ancient textual sources has shown that the process of salinization has a long history. Only the modern means to combat it are new: deep drainage to lower and hold down the water table, and utilization of chemical amendments to restore soil texture. In spite of the almost proverbial fertility of Mesopotamia in antiquity, ancient control of the water table was based only on avoidance of overirrigation and on the practice of weed-fallow in alternate

Dr. Jacobsen is a professor in the Oriental Institute, University of Chicago. Dr. Adams is an assistant professor in the department of anthropology and a research associate in the Oriental Institute, University of Chicago.