204

Grass Seminar

WASHINGTON UNIVERSITY

Student's Name D G Rogers

Course Seminar Btz 520

Section

Instructor or Assistant

Date Presented

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BOTANY 520.- SEMINAR OCTOBER 10, 1947

SEQUENCE OF TOPICS FOR DISCUSSION

		Rating	Rank
1.	Gross morphology. Anderson.	11	7
2.	Domesticated grasses. Sauer.	38	3
3.	Grasslands. Thomas, Schery.	53	2
4.	Epidermis. Meyer.	10	8
5.	Seedling. Rogers.	5	10
6.	Brewing. Pavcek.	14	6
7.	Vernalization. Commoner.	3	12
8.	Coleoptile. Richardson.	4	11
9.	Floral morphology. Van Schaack.	18	5
10.	Local grasses (Ecology--Schery)	36	4
11.	Evolution in the Gramineae. (Fossil record--Andrews) (Evolutionary patterns--Anderson) (Phylogenetic relations--Woodson)	59	1
12.	Diseases. Mehlquist.	7	9

The Gross Morphology of Zea Mays L. as an Example of Grass Morphology (Features of general significance in the Gramineae are underlined.)

A. Root system.

1. Primary roots--to be investigated.

2. Brace, prop, or nodal roots--appear immediately above node and push through sheath, rarely branch before reaching soil. Size is proportional to genotype and distance from ground, but is also greatly affected by length of day. Covered with slime at peak of growth.

B. Culm (haulm)

1. Main axis.

a. Nodes--(demonstration of morphology by Ko Ko Lay).

(1). Above the last ear--show no branching.

(2). Below the last ear--branching (as evidenced by prophylls).

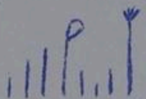
b. Internodes.

(1). Above the last ear--not grooved except for first node above the ear, not buckled.

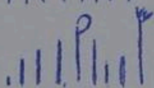
(2). Below the last ear--grooved in proportion to size of branch, buckled.

(3). Growth pattern.

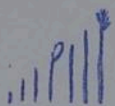
(a). Mexican dents:



(b). Corn Belt corn:



(c). Papago corn:



2. Branches.

a. Male inflorescence--terminal, not discussed in detail. (The dioecious habit is not common in grasses.)

b. Female inflorescence--an axillary branch, the development of which is proportional to the number of branching nodes it is from the base of the plant.

(1). Nodes--may give rise to tertiary branches (female inflorescences).

(2). Internodes--very short and sometimes very buckled.

c. Tillers--axillary branches rising from the base of the plant at the lowest nodes, the development of which is inversely proportional to the development of the inflorescence (and hence greatly affected by changes in latitude). There are considerable differences in tiller production between various streins of corn.

3. Leaves.

a. Husks or shucks--to be investigated by all.

b. Foliar leaves.

(1). Blade.

(2). Sheath.

(3). Ligule.

(4). Auricles.

c. Prophylls--characterized by having two keels and their position as first leaves of a branch. (Report by Holm on Arber's "pressure theory".)

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Continuation of Study of Zea Mays as an Example of Grass Morphology

1. Detailed consideration of tillers

    a. Importance in cereal grains.
    b. Importance in pasture grasses.
    c. Tiller differences in Mays

        1. Dent - no tillers.
        2. Flint - tillers.
    d. Tillers do not appear to increase production materially.
    e. Western Mexico and Hopi corn tillers produce normal sized ears.
    f. In Northern Flint corns tillers produce no or poor ears.

2. Stem leaves vs. ear leaves.

    a. Stem leaves (see last week).
    b. Husk leaves.
        1. Blades suppressed.
        2. Ligule present in many cases.
        3. Sheath dominant.
        4. Flag leaves characteristic of Northern Flints.

3. Mrs. Arbor's pressure theory.

    a. Grooves caused by pressure of branches when plant was in formative stage.
    b. Frequently the prophyllum is the only part of branch evident.
    c. No relation between grooving and buckling.
        1. Buckling in ear internodes great, no branches present.
    d. Pressure and the prophyllum.
        1. Report by R. W. Holm.
            A. The prophyllum of grasses and the importance of pressure in the development of grasses.
                1. In grasses, the prophyll and the palea are bikeeled or even bifid. This condition has been described as the result of the fusion of two leaves and also as the consequence of pressure on the growing organ. The morphological and anatomical evidence is as follows:
                    a. The prophyll has two prominent keels.
                    b. It is the first leaf of the axillary branch and, as such, is tightly pressed between the branch and the culm or rachilla.
                    c. In grasses the veins in the two keels are unequal in size.
                    d. The larger of the two is earlier in development, has an axillary bud opposite it, and is directly opposed to the median bundle of the next successive leaf.
                    e. Certain ligules, stipules, and bracts in other plants develop a bikeeled structure when they are pressed against the axis by another structure.
                    f. Palea lack the bikeeled structure when they occur in a terminal flower which is above the axis.

2. This evidence would indicate that the prophyll derives its bikeeled form from the pressure it experiences. Collins has reported, however, that two brahches are frequently found in the axils of the prophylls of certain Mexican corn and in a hybrid between maize and teosinte.

3. Pressure has been invoked to explain the structure of grasses since 1819 when Turpin used it to explain the absence of a back lodicule in certain species. Godron, Bugnon, and Arber believe that the effects of pressure on the organs of grasses in their embryonic stage are greater than is generally realized. The stem of a grass at an early age is very tightly enveloped by the series of overlapping sheaths of all of the leaves it will have. Because of the fact that there is but one prophyll in the monocots, it is caught, so to speak, between the axillant leaf and the stem; and it cooperates with the axillant leaf in an anterio-posterior pressure on the branch. This pressure on the floret results in the loss of the back lodicule and other modifications. (Sterilization of florets which is very common in grasses is not wholly explicable on this theory, however.)
(Arber, Agnes. 1934. The Gramineae. Cambridge Univ. Press. All references are here.)

4. Detailed study of nodal region.
   a. Report by Ko Ko Lay - Demonstration on nodes.

1. Nodes are highly specialized regions and they have definite zones for: (the following order from base up)
   a. Development of the leaves.
   b. Development of the buds.
   c. Development of the roots.
   d. The meristematic zone.

2. The position of the true node just beneath the false node.

3. Development of the roots. Usually all roots which succeed the radicle are borne on the nodes.

4. The meristematic area remains unlignified in most grasses long after flowering and retains the power of growth longer than other regions. The power of curvature of this region causes a lodged plant to be upright again.

5. The branching of vascular bundles usually occur as the strands enter the node. Few, if any, pass without branching. Interlacing and formation of net-work at the node. Later anastomosing with other smaller ones and joining up with the vascular strands.

PRELIMINARY LIST OF CULTIVATED GRAMINEAE
(Only species generally recognized in recent literature are listed)

I. GRAINS

SUBFAMILY POOIDEAE

Tribe Festuceae

Glyceria fluitans, R.Br.--Manna Grass
Eragrostis abyssinica L.--Teff

Tribe Aveneae

Avena strigosa, Schreb. (2n)--Hairy Oats
A. brevis, Roth. (2n)--Short Oats
A. abyssinica, Hochst. (4n)
A. sativa, L. (6n)--Oats
A. orientalis, Schreb. (6n)--Banner Oats
A. byzantina, C. Koch. (6n)--Red Oats
A. nuda, L. (6n)--Naked Oats

Tribe Chlorideae

Eleusine coracana, Gaertn.--African Millet

Tribe Hordeae

Hordeum vulgare, L. (2n)--Barley
Secale cereale, L. (2n)--Rye
Triticum monococcum, L. (2n)--Einkorn
T. Dicoccum, Schübl. (4n)--Emmer
T. durum, Desf. (4n)--Macaroni Wheat
T. polonicum, L. (4n)--Polish Wheat
T. turgidum, L. (4n)--Rivet Wheat
T. vulgare, Host. (6n)--Bread Wheat
T. compactum, Host. (6n)--Club Wheat
T. Spelta, L. (6n)--Spelt
T. sphaerococcum Perc. (6n)--Indian Dwarf Wheat

Tribe Oryzeae

Oryza sativa, L. (2n)--Rice

SUBFAMILY PANICOIDEAE

Tribe Paniceae

Digitaria sanguinalis, (L.)Scop.--Crab Grass
Panicum miliaceum, L.--Millet
Echinochloa frumentacea, Link.--Japanese Barnyard Millet
Setaria italica, Beauv.--Foxtail Millet
Pennisetum glaucum, R.Br.--Pearl Millet

Tribe Andropogoneae

Sorghum vulgare, Pers.--Sorghum

Tribe Maydeae

Coix Lacryma-Jobi, L.--Job's Tears
Zea Mays, L.--Maize

II. SUGAR-CANES

SUBFAMILY PANICOIDEAE

Tribe Andropogoneae

Saccharum officinarum, L.--Sugar Cane
Sorghum vulgare, Pers.--Sorghum

Tribe Maydeae

Zea Mays, L.--Maize

I I I. P E R F U M E S

SUBFAMILY PANICOIDEAE

Tribe Andropogoneae

Vetiveria zizanioides, Nash.--Vetiver
Cymbopogon citratus, Stapf.--Lemongrass
C. Nardus, Rendle.--Citronella Grass
C. Schoenanthus, Spreng.--Camel-hay
C. Martinii, Stapf.--Ginger Grass

MEMBERS OF THE SEMINAR

STAFF	GRADUATE STUDENTS
Anderson	Ayers
Andrews	Baxter
Commoner	Etter
Dodge	Hall
Lindegren	Holm
Mehlquist	Lay
Pavcek	Llano
Schery	Mamay
Van Schaack	McClary
Woodson	McQuade
	Meyer
Thomas	Morey
	Mundkur
	Ogden
	Raut
	Richardson
	Rogers
	Sauer

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I. Grasses used directly by man (only about 40 species).
    A. Textiles
    B. Fuels
    C. Perfumes
    D. Ornaments
        1. Horticultural grasses
        2. Job's Tears in Rosary
    E. Bedding
        1. Corn husk mattresses
        2. Straw ticking
    F. Paper
        1. Esperto grass
        2. Bamboo
    G. Shelter
        1. Bamboo
        2. Thatch
        3. Sod shanties
        4. Adobe bricks
        5. Insulation
            a. Bagasse (refuse of sugar cane)
    H. Food
        1. Flours and meals
        2. Oil
            a. Mazola
        3. Gruels
        4. Beverages
            a. Non-alcoholic
                (1) Parched cereals
                (2) Corn drinks
                (3) Tea grasses
            b. Alcoholic
                (1) Distilled
                (2) Non-distilled
                    (a) "Soak and rot"
                        1. Jap rice wine
                        2. Tepache le maiz
                        3. Rum
                    (b) Malting (sprouting to break down molecules)
                        1. Beer (barley)
                    (c) "Chew and spit"
                        1. Chicha - Prepared by Indians by chewing corn and collecting grindings which introduces diastase and yeast. Dried in sun, soaked overnight. Liquid decanted, refuse boiled down. Powdered dry sweet corn added, and also refuse syrup.
        5. Sugar and syrups
            a. Sugar cane
            b. Sorghum
            c. Corn
        6. Uses of the seed
            a. Popping
                (1) Internal pressure and water release
                (2) Only a few grains can be popped
                    (a) Corn
                    (b) Rice

b. Puffing
   (1) Release of pressure on outside
   (2) Most grains can be puffed
      (a) Rice
      (b) Wheat
      (c) Sorghum
c. Parching
   (1) Prevalent in pre-Columbian ear with Indians from St. Lawrence river to Bolivia
      (a) Pinol
         1. Made from corn or coix
d. Roasting
   (1) Corn
e. Immature cooked kinds
   (1) Corn
f. Food color (either stem or kernel used)
   (1) Hopi (N.A.) to Inca (S.A.) raise purple corn
      (a) Coloring drinks
      (b) Piki bread (Hopi and Zuni Indians)
         1. Corn flour made into dough and purple coloring matter added, making a pink dough. The dough is thrown onto hot rocks and cooks quickly. It looks like a pink parchment which is rolled into balls.

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I. Reports on Grass in Paper Making.

(1) The Origin and Development of "Rice Paper".

a. Early western users of this paper thought it made of rice because oriental in origin (Japan and Formosa, chiefly). Rice paper is not technically paper; it is made from pith of Aralia papyrifera. Orientals make paper similarly from phloem of Broussonetia papyrifera. Before 1521 Chinese made paper from rice straw. This paper will not bleach; it is used in ceremonies.
b. Three-fourths Chinese paper made from bamboo as follows: a pit is dug and lined with stones, bamboo is split and layered alternately with lime. After two months' soaking, bamboo is cleared, pulped, and molded in hand-molds.
c. In general, any rettable grass of high fibre content has been used to make paper some time or other. Today, bamboo, rice, straw, and esparto are the chief paper materials made from grass. See D. Hunter, Paper Making Through Eighteen Centuries. A. Knopf, 1943.

(2) Esparto Grass in Paper Making.

a. Stipa tenacissima is an outstanding paper constituent in Europe. Used for ropes, sandals, baskets, mats, cables. First used by the French, introduced into England in 1857, grows in poor soils in the Mediterranean Basin, is not a practical commercial crop. Good substitute for rags in paper. Used extensively in English bookmaking. Prepared by boiling mature dry leaves with caustic soda, washing and bleaching with chlorine.

II. Origins of Cultivated Grasses.

A. Cultivated plants have in many cases a very ancient history. How can origins be traced'

(1) Ethnological evidence.

a. Historical -- written and spoken information.

b. Philology, which in part is the tracing of common roots of names. De Candolle, Laufer, and E. D. Merrill have contributed to this.

Criticism of the philological approach is that it gives evidence of diffusion, but not necessarily evidence of origin. Examples:

Rye -- means "weed in the wheat". Was cultivated because it was able to establish itself in sites bad for wheat.

Plumeria -- tropical, ornamental. Called in the Philippines 'Apulco', the name probably derived from 'Acapulco', Mexico, where it probably originated.

(2) Archaeological evidence.

a. Extensive work done for the cultivated European wheats by the Germans.
b. Chronologies can be established through excavation of different levels in sections of deposition. This can be cross-checked by tree ring chronologies which are worked out by a cross-identifying technique. The only organisms which can be studied on this basis are the very resistant ones, such as corn, since perishable organisms are so ephemeral.

(3) Genetical evidence (Polyploidy).

a. Man can induce polyploidy by use of colchicine. An interesting question arises -- Do hybrids contribute anything new in evolution, or are they simply new combinations?
b. After hybrids are derived, the passage of time may bring about changes which make it difficult to trace their origins through the study of comparative morphology.
c. In many cases, resynthesizing can be accomplished, e.g., cotton, tobacco, wheat, and plums. A good example of what can be done in the study of cultivated plants is the "Evolution of Gossypium," by J. B. Hutchinson. "Vikings of Sunrise," by Buck, will go well with Hutchinson's book.
d. The chief criticism to the polyploidy technique of tracing origins is the criticism which applies to all of the sciences -- the monster specialization. Geneticists have opened the lock of the door into a very broad field, but the light is too bright for them to see clearly.

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(1) The Epidermis of Grasses.- Discussed by Dr. Henry Pratt of the University of Montreal.

A. Two basic types of epidermal cells.

(1) Early in development they are all isodiametric.
(2) Differentiate later into long and short cells.

B. Long(fundamental)cells.

(1) May be 200-300 times as long as wide.

C. Short(specialized)cells.

(1) Stomata formed of 4 cells from longitudinal division of a single short cell.
(2) Exodermic hairs(produced by short cells)
  a. multicellular
  b. bi-cellular
  c. cushioned.
(3) Exodermic spines(produced by short cells)
  a. small
  b. large
  c. cushioned
(4) Silicon cells.
  a. Formed by a transverse division of a short cell, the upper cell filling with colloidal silica which later solidifys.
  b. Shape of the silica cells vary and constitute a good taxonomic character.
  c. The lower cell(resulting from the same division forming the silica cell) becomes suberized.
  d. Both the silica cell and the suberous cell are dead and lack protoplast.

D. Types of Epidermal Tissues.

(1) Homogene(non-differentiated)
(2) Exodermique(with hairs and spines)
(3) Silico-subereux(silicon-suberous cells)

(4) The pattern of these tissue types is constant for different species and genera and seem to indicate phylo-genetic relationships, when closely similiar.

(5) As an example, Barley has the following epidermal pattern (as indicated by the numbers 1,2, and 3 given to the types listed above.)
Adaxial surface of leaf: sheath(3) - veins(2) - blade(1).-
Abaxial surface of leaf: sheath(1) - blade(1) - ligule(1) - base of veins(3) - top of veins(2).

(6) Leaves near the top of the plant have more type(3) than the lower leaves.

(7) Bamboo (one of the most primitive grasses) has probably the most highly differentiated epidermis, while some of the more modern genera are less differentiated.

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Origin and Spread of Cultivated Grasses (cont.)

I. Classes of Evidence

A. Evidence on phylogeny--biological relationships with wild relatives and between differentiates within the cultivated complex.
1. Comparative morphology
2. Anatomy
   a. Epidermis
3. Cytogenetics
   a. Analysis of individual character inheritance
   b. Analysis of ploidy
   c. Genom analysis
4. Physiology
   a. Chemical analysis
   b. Serology
   c. Disease resistance
   d. Environmental tolerances

(Concepts of phylogeny checked for consistency with evidence on chronology and diffusion.)

B. Evidence on chronology and diffusion--sequence of appearance and past and present distributions of both wild relatives and cultivated differentiates.
1. Archeology
2. History
3. Ethnobotany
   a. Techniques of cultivation and utilization
   b. Linguistics
4. Present distributions
   a. Distributions of taxonomic groups
   b. Analysis of populations and location of gene centers

(Concepts of chronology and diffusion checked for consistency with evidence on phylogeny.)

II. N.I. Vavilov

Interest in origins of cultivated grasses has largely arisen since De Candolle. Vavilov is one of major contributors. (See Dobzhansky's biographical sketch in current Journ. of Hered.) Vavilov trained in cereal breeding in England under Bateson. Directed most comprehensive studies to date of many cultivated plants in both Old and New Worlds.

A. Law of homologous variation. Parallel variation in independent groups; mutant genes produce similar characters in species which are not closely related. E.G. shattering and non-shattering inflorescences.

B. Gene centers. Dominant genes not distributed at random, usually concentrated in one or a few areas. Dominants, associated with wild plants, thus indicate centers of origin or diversification. Powerful technique, but requires caution, because concentration of dominants is affected by many factors other than time of occupance of an area.

III. Significance of Distributions.

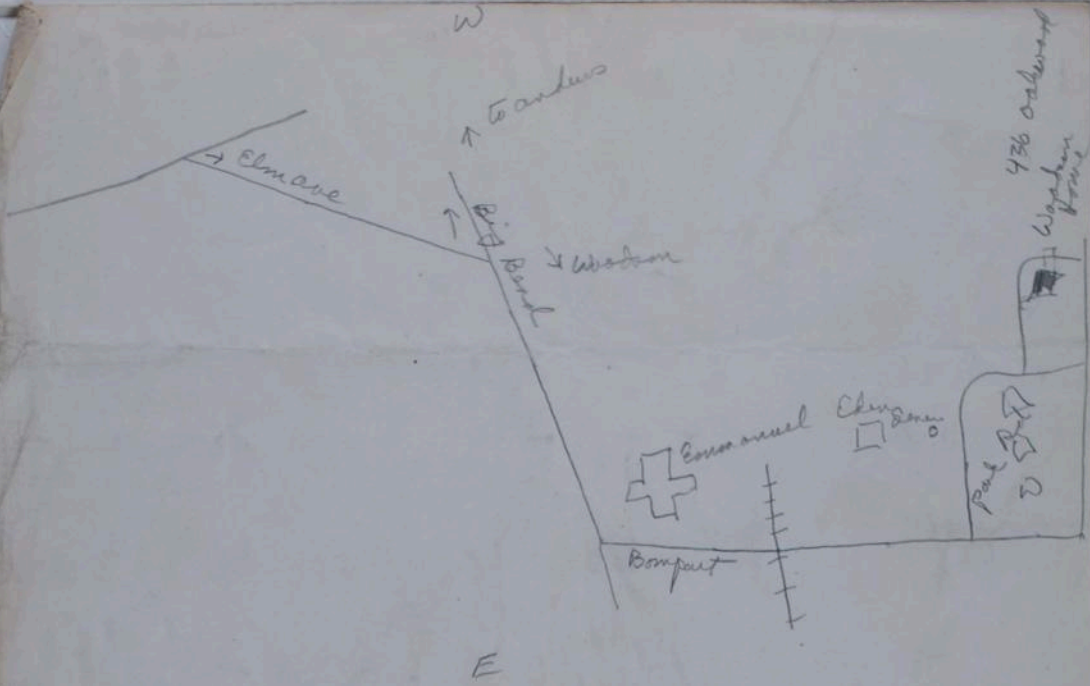
Distributions often used instinctively, without conscious philosophy of significance. They are significant in that they reflect the relationship of the plant to its environment. This relationship can be utilized in two ways: evidence on plant itself, or, in paleobotany and orthodox climatology,

III. Significance of Distributions (cont.)

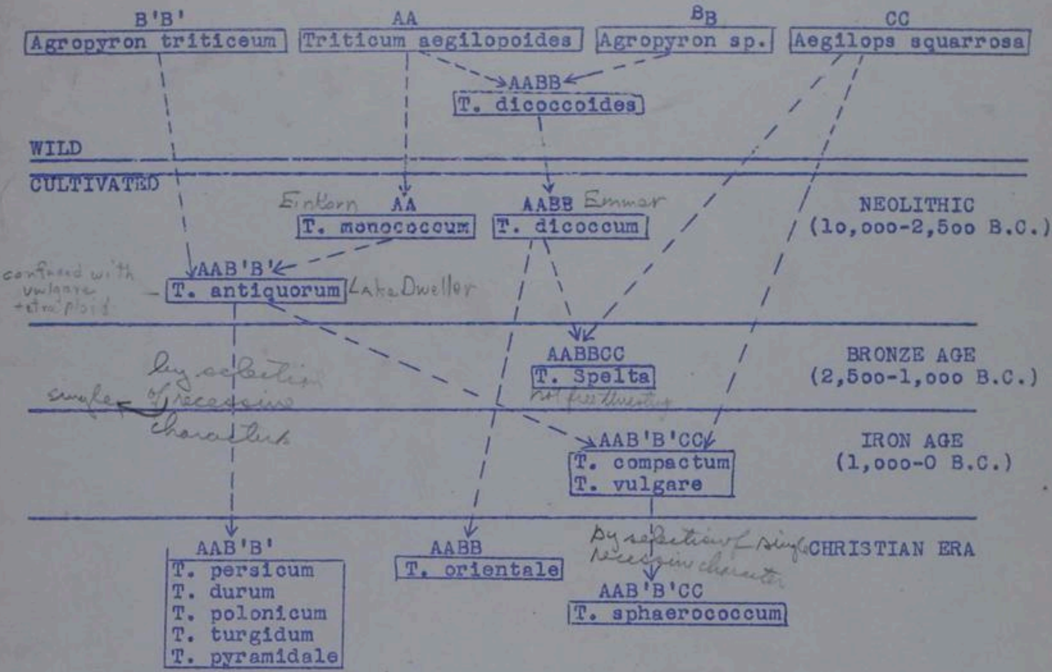
for evidence on environment. Plant distributions not at random but correlated with other variables, including other distributions. E.g., culture traits often correlated with plant distributions and aid in studying prehistory of plants. (Cf. Laufer, Hahn)

IV. Relative Importance of Different Kinds of Evidence

Depends partly on availability, largely on amount of variability in each type of evidence. E.g., in maize, sweet character based on single factor, may turn up anywhere; dent character based on multiple factor, may have originated only once. Sweet corn has very special uses; dent corn almost interchangeable with flint and flour corn. Thus, evidence on distribution of uses valuable in study of sweet corn, genetic evidence not valuable, while in dent corn the reverse is true.


W
Elm ave
Big Bend
Emmanuel
Bompart
E
436 Oakwood
Pool

TENTATIVE DERIVATION AND CHRONOLOGY OF WHEAT



Other ancient European cultivated grains:

Derived from Near East and S.W. Asia
Barley: Hordeum sativum--Neolithic
Oats: Avena fatua--Iron Age
Avena strigosa--Bronze Age
Rye: Secale cereale--Iron Age

Derived from Far East
Common millet: Panicum miliaceum--Neolithic
Italian millet: Setaria italica--Neolithic

No other cereals known in Europe until after beginning of Christian Era.

SEMINAR DISCUSSIONS ON GRASSLANDS

Topical order of coverage:

1. Definition and classification of grasslands

    a. Geography of grasslands - physical location
    b. Tropical grasslands
    c. Temperate grasslands

        1. Short grass
        2. Tall grass
        3. Mixed prairie

2. Grassland dynamics

    a. Climatic - climate, slope and altitude; (time?)
    b. Biotic - grasses and other organisms
    c. Edaphic - interplay grasses and soil types

3. Grasslands and man

    a. Grasses as weeds
    b. Man's effect on grasslands
    c. Future utilization of grasslands

        1. Private
        2. Nationalization

4. The evolution of grasslands

    a. Geological history
    b. Recent history

Authors and works worthy of review(and reviewer)

Weaver, et al. (Hall)
O. F. Cook
Stapeldon, et al. of Wales (Etter)
Sauer "Man and Grasslands" (Morey)
Gleason "Vegetational History of Middle West"
Transeau "Prairie Peninsula"
Dept. Interior "Range and Ranchlands of West" (Thomas)

Coverage dates:

March 19 - Thomas
April 9 - Thomas and Schery - development chernozem
April 16 - Schery and Hall
April 23 - Meyer
April 30 - Etter

May 7 - Ogden, Mamay and Baxter
May 14 -)
May 21 -) author reports
May 28 -)

GRASS SEMINAR 1947-48 - SEED AND SEEDLING

I. Importance of seed and seedling
   A. Use for specific studies--hormones and enzymes, morphological and biochemical studies.
   B. Used in study of phylogeny through comparative morphology.
   C. Use in commerce-starch, oil, malt, and digestive enzymes.

II. Morphology of seeds
   A. Parts--pericarp, remains of integument, nucellar membrane; aleurone layer; endosperm (starchy and horny); embryo.
   B. Embryo anatomy--three types distinguished by Van Tieghem, represented by Zea Mays, Avena sativa, and Triticum vulgare.
      1. Parts of embryo--scutellum (cotyledon?); axis of embryo; coleoptile; 3 nodes; elongated first internode (mesocotyl); scutellar node; primary seminal root; adventitious roots.
      2. Differences in types of embryos:

Zea Mays	Avena sativa	Triticum vulgare
1. No epiblast.	Epiblast.	Epiblast.
2. Primordia of seminal roots arising just above scutellar node.	Primordia at, or below the scutellar node.	Primordia in 2 pairs at scutellar node.
3. Procambium bundle of scutellum in upper and lower parts.	Procambium bundle in upper part only.	Procambium bundle in upper part only.
4. In dormant embryo, region between scutellar node and coleoptile elongated.	No elongation.	No elongation.
5. Epithelial glands in scutellum.	No epithelial glands.	No epithelial glands.
6. No "ventral scale" on scutellum.	"Ventral scale" overhangs coleoptile.	"Ventral scale" near apex of scutellum.

III. Physiology of seed.
   A. Corn.
      1. Two types of starch--hard and soft. Starch grains same structure differing in the surrounding protein network. Hard starch--heavy network; soft starch-fine network. Great problem in corn--how to get water out for good storage.
   B. Barley.
      1. Aleurone layer--proteins: hordine and glutenine (very insoluble in water)
         sugars: mono- and di-saccharides
         fats and sterols.
      2. Endosperm--proteins: glucosine (soluble in water)
         fats, sterols and starch.
      3. Husks--tannins and bitter resins.

IV. Physiology of seedling.
   A. Barley--processes of germination (malting).
      1. First step is absorption of water.
      2. Digestion of cell wall of endosperm and dissolution of intercellular matrix which holds starch grains together.
      3. Not all starch is completely disrupted, usually only starch next to epithelial layer is digested in first few days.

4. When wheat seedling with root 1 cm. long and maize 3 cm. long, sugar can be detected.
5. Epithelial layer, according to Sachs, passes enzymes to endosperm and re-passes sugar and proteins to embryo.
6. The process begins at contact of scutellum and epithelium.
7. Complete digestion of starch and proteins takes place only in later growth of seedling.

B. Theories of digestion.
1. Old school.
   a. To a secretion of endosperm itself.
   b. To a secretion of aleurone layer.
2. Modern school.
   a. To a secretion by epithelial layer of scutellum.
   b. Proof of this theory.
      1. The grain minus embryo--no digestion.
      2. Scutellum part of embryo alone--will digest starch.
      3. Removal of epithelial layer--no digestion.
      4. Aleurone layer not too involved in digestion--made of living cells which live on after starch in digested. Function of aleurone--to prevent entry of bacteria and fungi. It has a high concentration of thiamin and flavine.

Starch in endosperm ⇄ (Enzyme) Sugar and Amino Acids → epithelium → scutellum → embryo-resynthesis for germinating tissue.

V. Variation in seed composition in the Graminese.
A. In practically all seeds of grasses, the embryo is small, therefore it is not completely true that man seems to have made endosperm large, but probably the whole grain large. In general, cultivated grains are much larger than their wild relatives.

VI. Anatomy of corn seedling.
A. Primary root.
1. Essentially the same as the primary root of all grasses.
2. Anatomically, lateral seminal roots similar to primary root, except that they are smaller and have fewer protoxylem points.

B. Adventitious roots.
1. Essentially same as earlier seminal roots, but much larger, and frequently have as many as 48 protoxylem points.

C. Seedling axis.
1. Transition from exarch xylem of root to endarch xylem of stem begins at vascular plant of scutellar node, and continues upward through first three or four internodes.
2. Elongation of first internode accomplished by meristematic activity at the topeof the internode, rather than at base of internode, as in higher internodes.
3. Second internode not elongated in embryo, but consists largely of meristematic tissue.

VII. Wheat seedling.
A. Varies but little from oats and corn.
1. First internode is not elongated, but second internode becomes elongated on germination.

VIII. Bibliography.

1. Avery, G. S. Jr., Comparative Anatomy and Morphology of Embryos and Seedlings

of Maize, Oats, and wheat, Bot. Gas. 89: 1-30, 1930--A consideration of the problems raised by Sargant and Arber. Disagrees with them in part as to interpretations.

2. Corn in Industry, Corn Industries Research Foundation, 5 E. 45th St., New York--Excellant propaganda booklet, summarizing uses of maize in modern United States industry.
3. Harlan, USDA 180, 1916--Summary of the morphology and physiology of germination in barley.
4. Kennedy, P. B., USDA (Agrostology) 19, 1899-1901--Survey of sizes and shapes of endosperm and embryo in various grasses, Numerous line drawings.
5. McMasters and Cox--Study of hard and soft starch as digested by wet milling process.
6. Sargant and Arber, Ann. Bot. 29; 1915--Anatomical investigation of Zea, Avena, and other grasses. largely concerned with homologies between grass seedlings, and those of other plants. Many clear anatomical illustrations.
7. Van Tiegham, Ann. Sci. Nat. Bot. V, 15, 236-276, 1872. Ibid, VIII, 3, 1897--One of first critical studies of morphology of grass seeds and seedlings.

GRASS SEMINAR 1947-48 - SEED AND SEEDLING

I. Importance of seed and seedling
   A. Use for specific studies--hormones and enzymes, morphological and biochemical studies.
   B. Used in study of phylogeny through comparative morphology.
   C. Use in commerce-starch, oil, malt, and digestive enzymes.

II. Morphology of seeds
   A. Parts--pericarp, remains of integument, nucellar membrane; aleurone layer; endosperm (starchy and horny); embryo.
   B. Embryo anatomy--three types distinguished by Van Tieghem, represented by Zea Mays, Avena sativa, and Triticum vulgare.
      1. Parts of embryo--scutellum (cotyledon?); axis of embryo; coleoptile; 3 nodes; elongated first internode (mesocotyl); scutellar node; primary seminal root; adventitious roots.
      2. Differences in types of embryos:

Zea Mays	Avena sativa	Triticum vulgare
1. No epiblast.	Epiblast.	Epiblast.
2. Primordia of seminal roots arising just above scutellar node.	Primordia at, or below the scutellar node.	Primordia in 2 pairs at scutellar node.
3. Procambium bundle of scutellum in upper and lower parts.	Procambium bundle in upper part only.	Procambium bundle in upper part only.
4. In dormant embryo, region between scutellar node and coleoptile elongated.	No elongation.	No elongation.
5. Epithelial glands in scutellum.	No epithelial glands.	No epithelial glands.
6. No "ventral scale" on scutellum.	"Ventral scale" overhangs coleoptile.	"Ventral scale" near apex of scutellum.

III. Physiology of seed.
   A. Corn.
      1. Two types of starch--hard and soft. Starch grains same structure differing in the surrounding protein network. Hard starch--heavy network; soft starch-fine network. Great problem in corn--how to get water out for good storage.
   B. Barley.
      1. Aleurone layer--proteins: hordine and glutenine (very insoluble in water)
         sugars: mono- and di-saccharides
         fats and sterols.
      2. Endosperm--proteins: glucosine (soluble in water)
         fats, sterols and starch.
      3. Husks--tannins and bitter resins.

IV. Physiology of seedling.
   A. Barley--processes of germination (malting).
      1. First step is absorption of water.
      2. Digestion of cell wall of endosperm and dissolution of intercellular matrix which holds starch grains together.
      3. Not all starch is completely disrupted, usually only starch next to epithelial layer is digested in first few days.

4. When wheat seedling with root 1 cm. long and maize 3 cm. long, sugar can be detected.
5. Epithelial layer, according to Sachs, passes enzymes to endosperm and repasses sugar and proteins to embryo.
6. The process begins at contact of scutellum and epithelium.
7. Complete digestion of starch and proteins takes place only in later growth of seedling.

B. Theories of digestion.

1. Old school.
   a. To a secretion of endosperm itself.
   b. To a secretion of aleurone layer.
2. Modern school.
   a. To a secretion by epithelial layer of scutellum.
   b. Proof of this theory.
      1. The grain minus embryo--no digestion.
      2. Scutellum part of embryo alone--will digest starch.
      3. Removal of epithelial layer--no digestion.
      4. Aleurone layer not too involved in digestion--made of living cells which live on after starch in digested. Function of aleurone--to prevent entry of bacteria and fungi. It has a high concentration of thiamin and flavine.

Starch in endosperm ⟷ (Enzyme) Sugar and Amino Acids   epithelium ⟶ scutellum ⟶ embryo-resynthesis for germinating tissue.

V. Variation in seed composition in the Graminese.

A. In practically all seeds of grasses, the embryo is small, therefore it is not completely true that men seems to have made endosperm large, but probably the whole grain large. In general, cultivated grains are much larger than their wild relatives.

VI. Anatomy of corn seedling.

A. Primary root.
   1. Essentially the same as the primary root of all grasses.
   2. Anatomically, lateral seminal roots similar to primary root, except that they are smaller and have fewer protoxylem points.

B. Adventitious roots.
   1. Essentially same as earlier seminal roots, but much larger, and frequently have as many as 48 protoxylem points.

C. Seedling axis.
   1. Transition from exarch xylem of root to endarch xylem of stem begins at vascular plant of scutellar node, and continues upward through first three or four internodes.
   2. Elongation of first internode accomplished by meristematic activity at the topeof the internode, rather than at base of internode, as in higher internodes.
   3. Second internode not elongated in embryo, but consists largely of meristematic tissue.

VII. Wheat seedling.

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The commonly spoken of seed in the family Graminea is actually the mature fruit or caryopsis, in chich the seed coat or tests has become so closely invested by the pericarp as to appear fused with it.

Most critical studies of the anatomy of the caryopsis have been done on the cultivated grasses, but the study of any one can give us a general picture of them all, since the only variance is in size and shape, rather than in difference of parts. Corn, for example, has been studied assiduously, as have been oats, wheat, rice, etc.

The mature grain consists of the hull, which is made up of the pericarp, remains of the integuments which may be present or absent, the nucellar membrane, the aleurone layer, the starchy endosperm, and the embryo. The stalk at the base of the grain is the pedicel, The point of attachment of the silk of corn may be seen as a small bump or depression on the side of the grain where the embryo is.

The pericarp is composed of several layers, the outer layer or epicarp consists of elongated cells with a well-developed cuticly on the outer face. The mesocarp, or next inner layer has much the same construction as the epicarp, except that the cell walls are thicker. The next layer,is composed of parenchyma with large intercellular spaces. Adjacent to the parenchyma, and forming the inner layer of the pericarp, is a layer of tube cells. These cells are drawn apart as the grain matures, forming a net-work over the inner face of the pericarp.

The integuments are rather poorly developed, and at maturity are crushed or resorbed. In some cases however, the inner integument persists, being two-layered, except near the micropyle, where there may be 3-5 layers.

Weatherwax has called this layer the testa, but Randolph, in a study of the variety Pride of Michigan concluded that "the maize caryopsis has no true seed coat".

The nucellus in the mature grain consists largely of disintegrated cellular remains forming a suberized membran between the pericarp and aleurone layer.

The endosperm is composed of the aleurone layer and the starchy endosperm. The cells of the aleurone layer are cubicle, thick-walled, and generally only one layer thick. However, by periclinal division, they may become two layers thick. The layer of the endosperm immediately beneath the aleurone layer has cells giving it the appearance of a horny substance. These cells are higher in protein content than the starchy endosperm. The amount of horny and starchy endosperm is variable, depending on the variety. Thruout the endosperm there are strands of material of a protein nature which forms a network.

Anatomy of the Embryo of Gramineae

There are three main morphological types of embryos in the Graminaea distinguished by Van Tieghem--Zea Mays L., Avena sativa L., and Triticum Vulgare Vill. Of these, I have chosen corn to discuss in detail, and will compare it with both Avena and Triticum. to show the variance between them.

Historically, little critical work was done on the anatomy of the embryo prior to ~~when~~ 1872 when Van Tieghem published his first study of the anatomy of the embryo of certain grasses. He renounced certain of the ideas given in this work in another appearing in 1897. According to Van Tieghem, the scutellum was the 1st cotyledon, the epiblast representing the rudimentary second cotyledon. To him the coleoptile was the 3rd leaf superposed to the scutellum or first leaf, and the 1st green leaf superposed to the epiblast was the 4th leaf of the plant.

Schlickum considered the scutellum and coleoptile to be the cotyledon.

Celakovsky, thought that the scutellum was homologous to a blade of grass, (agreeing in part with the earlier published works of Van Tieghem) the coleoptile as the sheath, ~~givingxtoxthexregionxwhichxjoinsxthextwoxthex namexmesocotyls.~~ He considered the epiblast to be an appendage to the scutellum, comparable to an auricle, as is found at the base of some blades of grass.

Coulter thought that in the evolution of monocots ~~to~~ from dicots, there was a suppression of one cotyledon. He cited maize and other members of the monocot families as showing that the epiblast was the 2nd cotyledon, which attained only a rudimentary stage of development. The scutellum represented the one remaining functional cotyledon.

Sargant and Arber thought the cotyledon to consist of a sucking apex (the scutellum) and a sheath (the coleoptile); the latter being perhaps equivalent to a pair of stipules. The epiblast was considered to be an outgrowth of the cotyledon, of the axis, or of both, and as being of little morphological significance.

Others have had various interpretations, but none of any particular significance.

These authors were particularly interested in the embryo, and the discussion has delt only with the embryo. The following discussion deals with the seedling, and in particular, that portion of the axis which in corn lies between the scutellum underground, and the node at the surface of the ground where the coleoptile diverges from the axis. This structure is equally evident in oats as in corn, but that in wheat is much less conspicuous.

This portion of the axis has been studied in some detail by various authors, the first among them being Clos who saitisfied himself by calling it simply a "neck". Van Tieghem was the first who made a careful study of the structure. His view was that the structure is an elongated first node, belonging neither to the epicotyl or to the hypocotyl. DeBary was the first to consider the structure in question an internode. Celakovsky, in complete agreement with Van Teighem's earliest work, considered the region to be an elongated node, and was the first to give the structure the name "mesocotyl". Sargant and Arber regorded the region as having resulted from a fusion of the cotyledonary stalk with the hypocotyl, and thus neither a node nor an internode. Other authors have either agreed with Van Tieghem or with a gentlement named Bruns, whose interpretation ~~xx~~ was much the same as DeBary's internode.

Now that we have discussed the historic al aspects, we can begin to consider the structures which were in question. The embryo lies imbedded in the endosperm, on one side and toward the base of the caryopsis, with the lower end towards the base ~~ofxthexxx~~ Looking at the longitudinal section, (Slide 1) the upper part of the axis may be seen to consist of nodes bearing the primordia of leaves. The internodes are unelongated. There is a short neck-like interval in the axis between the levels of divergence of the embryonic leaves and that of the scutellum. The apex of the axis consists of a small growing point. The embryonic leaves and growing point are covered by the coleoptile, and approximately cone-shaped structure. In longitudinal-face section (slide 2) you can see the primordia of two or more adventitious roots arising in the region just above the scutellar node. As you can see, they are directed laterally upward.

(Slide one again, please)

The scutellum is a prominent structure attached to one side of the axis. Largely of parenchyma, it has a prominent layer of epithelial cells in contact with the endosperm tissue during germination. (Fig Slidexxi) The epithelial layer often has infoldings in its surface, which have been described by Sargant and Robertson as epithelial glands.

The embryonic vascular system consists partlyxofxa partly of a large procambial strand laid down in the scutellum. Its method of branching may be seen on the slide. The upper and lower bundles joine at the level of divergence of the scutellum from the axis and within the embryonic axis are connect ed directly with the stelel. Continuing from the place of attachment of the scutellum bundle to the stele, one can easily trace procambial elements to the first leaf above the coleoptile. The vascular bundle of the coleoptile consists usually of two vascular bundles one on either side. They arise directly from the stele of the embryonic axis, at the upper end of the necklike interval in the axis.

At the lower end of the embryo may be seen the root cap, the primary rootand the coleorhiza. Slide 3, please.

The structure of the embryo of Avena is very similar to that of Zea, but much smaller. The scutellum much exceeds the embryonic axis in length, is slender, and has a sharply convex face toward the endosperm. Com pared with the maize embryo, it differs in the following six respects: (1) There is an epiblast(slide 3) (2) the primordia of the seminal roots other than the primary root appear in, or slightly below the region of the scutellar node, being directed laterally downward. (3) The large procambial bundle in the scutellum shows small branch strands divergin from the upper part of the main trunk, with the appearance of a fan whose ribs are bent over toward the handle, and no development in the lower part of the scutellum. (4) In the dormant embryo there is no elongated interval in the axis between the scutellum and the coleoptile. (5) The epithelium of the scutellum has not been observed to possess infoldings in its surface, and (6) On the ventral face of the scutellum is the "ventral scale", a small protrusion of tissue a considerable distance down from the apex and slightly overh anging the coleoptile.

The embryo of wheat varies but little from that of Avena. They both possess epiblasts, similar scutellar, and axial vascular systems. The points of difference are: (1) The primordia of the seminal roots, excludi ng the primary root, occur in two pairs. They appear in the region of the scutellar node, being directed laterally downward. These may be seen in slide 2. (2) The scutellum is a short structure, extending only slightly beyond the tip of the coleoptile. Its ventral scale is therefore near its apex.

Since it is rather difficult to determine the nature of the tissues, both vascular and non-vascular, in the dormant embryo, much study has been devoted to the seedling in grasses for detailed anatomy. The remaining portion of this discussion will concern the anatomy of the seedlings of the same tyggggdiscussed previously.

general

Again, the most detailed discussion will deal with the seedling of corn, with comparisons of it to that of Avena and Triticum.

The primary root has a pith composed of large parenchymatous cells, isodiametric in trasverse section, consitituting the larger portion of the stele. The pith cells about the metaxylem vessels become thick-walled with in ten days after germination. The number of protoxylem points varies from eighte en to more than twice that number. There is usually one large metaxylem vessel for each two or three protoxylem groups. Alternating with the protoxylem groups are groups of phloem, each usually composed of several cells. Kext The pericycle is characteristica ly a single layer of cells.

Most of the cells of the endodermis have their entire inner tangential walls conspicuously thickened. The epidermis is lost early, and t he walls of the outer few layers of cortical cells often become thickened. This thickening does not take place to any marked degree, however, until after the root hairs have become functionless; it is simultaneous with the thickening of the wa ls of certain cells of the pith, already described. Anatomically the roots arising from the axis just above the level of attachment of the scutellum are similar to the primary root. They deffer in being smaller and having fewer protoxylem points.

The structure of the first adventitious roots to appear at the surface of the ground is essentially the same as that of earlier seminal roots. They become much larger, however, and frequently have as many as fort-eight or more protoxylem points.

Slide 4

Seedling Axis: The first step in the "transition" from the exarch condition of the xylem of the root to the endarch condition of the xylem of the stem takes place in the vascular plate at the scutellar node. (see slide 4.) In addition, the interval in the axis between the level of divergence of the scutellum and that of the coleoptile is a transition region. Exarch exylem groups may be observed as far up as the divergence of the coleoptile.

The axis above the scutellum is partly sheathed at its lower end by the scutellum . In transverse section it resembes the primary root., in having small exarch exylem groups. There are, however, fewr of these groups. There is a large pith of thin-walled isodiametric parenchymatous cells. In addition, bet ween the exarch ex xylemgroups are endarch collateral bundles whose phloem alternates wit h the exarch xylem groups. The collateral bundles are not as shorply defined as are those in the upper internodes. The endarch and exarch bundles are arranged in a circle just inside the periphery of the stele, similar to the circle of vascular tissue in the root. Ordinarily exarch groups and endarch bundles occur alternately, or there may be two or more endarch bundles separating successive exarch groups. The pericycle is easily identified as the prominent layer of cells immediately within the endodermis. Adventitious roots may arise from the pericycle at any level betwwen the scutellum and the coleoptile. The radial and inner tangential walls of the endodermal cells are heavily thickened. The cortex is several cells in thickness; surrounding it is a layer of epidermal cells whose outer walls are lightly cutinized. The walls of one or more layers of cortical cells beneath the epidermis are aften slightly thickened.

The interval on the axis between the scutellum and the coleoptile (called at present xxxixx the first internode) elongates by means of division and enlargement of cells just below the level of divergence of the coleoptile. You will recall from Mr. KoKoLay's discussion earlier this year that in the higher innner nodes, the meristematic region at the base of the internode causes elongation.

The vascular supply of the coleoptile diverges from two bundles x that occur on the side of the stele toward the scutellum. At the level of the coleoptilar node, approximately half of each of these bundles diverges laterally outward into the coleoptile. The remaining half of each bundle continues upward in the axis, giving rise to one or more traces to the leaf above the coleoptile. Only minor variations have been observed to take place in the origin of the vascular supply of the coleoptile and of the leaf next above it. It is obvious that the bundles of t he coleoptile are ordinary leaf traces from the stele. The internode between the coleoptile and the foliage leaf next above it is sheathed by the coleoptile and differs anatomically from the higher internodes. It possesses a rather thick cortex, very indefinite and poorly defined bundles, and an almost continuous sheath of meristematic cells among which may be found some differentiated xx xylem and phloem. While no particular study has been made of this meristematic sheath, it would appear to be of pericyclic origin. T he internodes above the second and third foliage leaves resemble more closely the higher internodes.

Coleoptile: The coleoptile has already been described as sheathing the growing point and embryonic leaves during the early stages of germination, and as being elevated by the growth of theelongating axis. It has also been described as having commonly a vascular system composed of two bundles, one on either side. The origin of the coleoptile traces has been described.

There are exceptions to the usual numbe r of vascular bundles in the coleoptile. Avery has reported the presence of as many as five bundles. The extra bundles have ordinarily an origin similar to that of the usual two, although in the case of five, the fifth bundle usually arises de novo in the cortex below the coleoptilar node.

In transverse section the coleoptile displays a very simple structure, being largely parenchymatous. The vascular bundles are large. Each bundle has many xylem groups and a considerable amount of phloem tissue. The parenchyma making up the body of the coleoptile is closely arranged, having only small intercellular spaces. Stomata are present only in the outer epidermis. They are usually confined to one or a few rows on either side of the two vascular bundles. The guard cells are small, as are the air spaces beneath them. Chloroplasts are most numerous in the region of the bundles.

~~Axbudxwz~~
Buds are present in the axil of the coleoptile rather infrequently. Avery states that the presence of a bud appears to depend largely upon moisture and temperature conditions at the time of germination.

Foliage leaves: Structurally the later foliage leaves of corn are typically similar to an ordinary grass leaf, being composed of a sheath and blade.

In the seedling of Avena, as contrasted with Zea, the following differences occur. ~~Thexprimaryxrootxhasxaxsinglexlargexmetaxylemxvessel,xshowingxmagnifiedxwallxwithin~~
In the root ~~anfxenmiayax~~ The number of protoxylem points of the polyarch xylem varies, seven and eight being the most common numbers, whereas in corn, the number of proxylem points is eighteen. The transition zone in Avena is rather abrupt,~~ix~~ as in corn, and much the same process occurs. Above this abrupt transition region is a transition interval which extends from the level of divergence of the scutellum to th at of the coleoptile. The elongation of this interval with a diagramatic view of internal development may be observed in figs. 25-27, slide 4. The location of the meristematic region in this interval is similar to that in maize. However, when elongation takes place it is seen to be slightly different, being above the vascular plate at the scutellar node and su rounding the scutellar bundle, Therefore the scutellar bundle in the seedling axis extends upward parallel to, but does not become part of, the stele until it reaches the level of divergence of the coleoptile.

At the level of divergence of the coleoptile, the scutellar bundle forms part of the stele and turns downward within it. At th is point two branches diverge from it which extend first laterally and then upward in the axis. As they extend upward each branch in turn diverges. These last two trace s thus derived, one on either side, are coleoptilar bundles. Sargant and Arber descri be the same situation by saying that half of each coleoptile bundle arises from the stele. Even though this is apparently ture, the half coming from the stele comes from the same scutellar bundle that has turned downward within it. ~~Longitudinalxfarxsectionxofxthex~~ The scutellar bundle is entirely responsible for two (more often four)bundles of the leaf above the coleoptile, in addition to being partly responsible for its midrib. In a similar manner some of the traces of the second leaf above the coleoptile may be traced in their origin back to the scutellar bundle.

Theinternode between the coleoptile and the next foliage leaf is sheathed by the coleoptile. It differs anatomically from the hi her internodes. It too is a transition interval, being more like the higher internodes than the internode next below it.

Coleoptile: The coleoptile isx structurally similar to that of maize, although much smaller, being about the size of that of what. It differs from the coleoptile of corn in the following respects: (1) the vascu lar bundles are small, with few xylem groups and relatively abundant phloem; (2) a bud is almost universally present in the axil of the coleoptile; (3) no more than the usual two vascular bundles have been observed in the coleoptile.

The Seedling of wheat: The most striking difference between the seedling of wheat and the two previously described is that the part of the axis between the level of divergence of the scutellum and that of the coleoptile (the first internode) is very short. A slight elongation takes place in this region as the seedling develops, but the principal region of elongation in the young wh eat axis is the internode above the coleoptile shown in fig 35, slide 4.

The scutellar bundle within the axis di verges (frequently extending upward in the axis for a short distance before becomign part of the stele,(fig 35, slide 4)), the central third of it becoming part of the stele directly. Each outside divergence extends laterally upward for a short distance, then again diverges into two bundles, the outer one of each pair being a coleoptile trace. Th e inner bundle of each pair extends upward in the axis and finally diverges, giving rise to one or more bundles of the leaf above the coleoptile, as in the oat. The central third of the original scutellar bundle may be traced downward in the stele to the vascular p late at the scutellar node, where it turns upward. At this level a few vascular strands from the root add to it, and it extends upward in the stele, finally diverging as the midrib of the leaf above the coleoptile. The scutellar bundle is, therefore, entirely responsible for at least two bundles of the leaf above the coleoptile and partly responsible for its midrib.

The internode between coleoptile and th e next foliage leaf is approximately the same as in corn and oats.

The coleoptile of wheat in contrast to those of corn and oats, is not elevated (or only slightly so, as already pointed out) by a growth of the elongating axis, but instead, itself sheathes the elngating axis. The coleoptile has been observed (Avery) to reach a length of more than 4 inches.

The foliage leaves present the same paterns as those of corn and oats.

Summary

1. The scutellum in maize, oats, and wh eat is the cotyledon. The "ventral scale" of the cotyledon, when present, may be interpreted as its ligule. The epiblast, when present, xxxxxx cannot be considered a rudimentary cotyledon; it probably has little morphological significance. These interpretations hold also for other grasses, including barley, rye, and rice.

2. The coleoptile is homologous with a foliage leaf, and is the second leaf of the plant, the leaf distal to it being the third leaf of the plant.

3. In maize and oat seedlings, the elon gated structure between the cotyledon and the coleoptile is the first internode of the axis. The term "mesocotyl" as applied to this structure is meaninglesss. In wheat, the corresponding structure, although not elongated, is likewise the first internode of the axis. This holds true for other Gramineae that develop similarly to maize, such as oats and rice, and those that develop like wheat, such as barley and rye. The principal elongating structure in the young wheat axis is the second internode. It is always sh eath d by the coleoptile.

4. There is no hypocotyledonary region of "transition" in the grasses. The transition is confined to stem structure. It starts and takes place largely in the vascular plate at the first node, and in the first internode. The transition continues in the second internode, and to some degree even in the third and fourth internodes.

5. The three morphological types distinguished by Van Teighem are fundamentally one type, appearing differently upon development because of the difference in location of the meristematic region in the first internode. These differences often show in the mature embryo, before germination begins. The similarity of the vascular skeletons has been pointed out.