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THE STRUCTURE OF THE RHIZOMES OF
AGROPYRON REPENS, BEAU., POA PRATENSIS
L., AND FESTUCA ARUNDINACEA SCHREB.,
VARIETY ALTA.

The Ohio State University, Ph.D., 1965
Botany

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THE STRUCTURE OF THE RHIZOMES OF AGROPYRON REPENS, BEAU.,
POA PRATENSIS L., AND FESTUCA ARUNDINACEA SCHREB.,
VARIETY ALTA

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

by

Jagdev Singh Sawhney, B.Sc.(Hons)Ag., M.S.

.........

The Ohio State University

1965

Approved by

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Department of Botany and
Plant Pathology
ACKNOWLEDGMENTS

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I am very grateful to Miss Diana L. Heckman for typing and retyping the manuscript.

Lastly, I wish to express my sincere appreciation to my wife, Phulinder, for many long and lonely hours she spent during the course of this investigation.
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FIELDS OF STUDY

Major Field: Crop Physiology and Morphology


Studies in Plant Physiology. Professors C. A. Swanson, B. S. Meyer, R. S. Platt, and J. W. A. Burley
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INTRODUCTION

Tall Fescue, *Festuca arundinacea* Schreb., is a cool season multipurpose grass. It has been used in forage mixtures with various clovers, in turf mixtures with Kentucky bluegrass, *Poa pratensis* L., for erosion control on roadcuts and berm protection, and for other soil conservation measures. It is a very aggressive grass and can stand a lot of misuse, e.g., in playgrounds and wet areas as well as in such poor fertility situations as highway right of ways. It is claimed to be able to resist alkaline and acid conditions, as well as the freezing and thawing, better than many other grasses.

Tall Fescue is a bunch-type grass. It reproduces by seed and by the formation of tillers. The tillers are the shoots formed by the sprouting of the buds in the axils of the leaves of the main stem of the plant derived from the seed or the plant material used for getting the stand in the first place. Most of the shoots derived from the tall fescue plants are of this type, and the base of the original plant is sometimes referred to as the crown. If this crown of the tall fescue is killed, e.g., by mismanagement, winter injury, drought, etc., the entire plant dies. This type of damage done to the turf results in the thinning of the stand of the tall fescue turf with the passage of time. This method of vegetative reproduction, the tillering, makes this grass
less suitable for the uses to which it is put. If a rhizomatous variety or strain of this grass can be found, it will improve to a great extent its present characteristics.

Porter (24), a soil conservationist, found a few rhizomatous plants of tall fescue in the United States Soil Conservation Service, Plant Materials Centre, at Big Flats, New York. On a survey of the old stands of tall fescue on the University Farm of The Ohio State University and on the interstate highway, I-71 right of way, some plants with structures morphologically similar to rhizomes were found.

The objectives of the present study were:

1. To determine the structure of a rhizome.
2. To determine the structure of rhizome-like organs of the tall fescue plants.
3. To determine the basic similarities of the rhizomes as opposed to the aerial stems of tall fescue, Kentucky bluegrass, and quackgrass.
4. To find out the origin of the "rhizomes" of tall fescue.

In order to attain these objectives, three grasses—tall fescue, Kentucky bluegrass (*Poa pratensis* L.), and quackgrass (*Agropyron repens* Beauv.)—were used in this study. Kentucky bluegrass and quackgrass were selected because both of them have well-developed rhizomes underground on the same plants and typical aerial stems. The formation of rhizomes in relation to ground surface is, however, different in these two grasses. While the rhizomes of quackgrass develop underground, the rhizomes of Kentucky bluegrass
are formed above ground and then go underground. It is also the purpose of this study to determine whether the difference in origin of the rhizomes of the two types of grasses has any effect on the internal structures of the rhizomes.
What is a rhizome?

The term rhizome was first introduced into the biological literature by Erhart (6). Since then various botanists have used this term and each one has tried to define it while using it for some explanation or discussion. The approach to the definition has been the physiological one, that of geotropism or its growth in relation to the surface of the soil. Sometimes the structural details have been mentioned without giving the specific characteristics which differentiate them from the other morphological forms of the stem.

The first definition of the rhizome was given by Link (18). He called the stems originating underground or "basis caulis intra terrain demersa," the rhizomes. Eight years later, Lindley (17) defined rhizomes as prostrate thickened rooting stems. The underground nature of the rhizomes was emphasized by De Condolle (5) by the term "cache sous terre." By the year 1836, it was very well agreed that rhizomes were "tiges-souterraneae et horizontal," or underground and horizontal stems (28).

Holm (14) reviewed the old literature on the term rhizome. According to him, all underground stems were rhizomes whether they were horizontal or vertical, homogenous or heterogenous, monopodial or sympodial, and root bearing or rootless. He distinguished the
rhizomes from the stolons in that the structure of stolons was
different from the stems on which they were borne, while the
rhizomes had the same structure as the main axis. He did not,
however, elaborate on the differences in structure. The structure
of rhizomes, stolons, and aerial stems was found to be identical
by Arber (1), as reported in one of the first few books on
Gramineae. She indicated that these three organs differed from
one another only in their physiological growth response to gravity,
called geotropism. The rhizome had the characteristic underground
habitat; various intermediate forms of horizontal rooting axis
between the aerial stem and the rhizome exist (1, 20). Arber (1)
indicated that "the horizontal rooting axis may become subter-
ranean rhizomes producing one or more aerial shoots in a tuft or
in succession; they also might become above ground stolons ending
in one or more flowering shoots."

While the underground nature of the rhizomes had been
accepted (9, 16), doubt still existed about whether the rhizomes
were rooting stems (9) or were without roots (16). The rhizomes
had internode extension (16) and might arise above or below the
surface of the ground (9). The well-known rhizomes of Kentucky
bluegrass and the reed canarygrass, Phalaris arundinacea, differed
in their origins in relation to the soil surface. While the
rhizomes of Kentucky bluegrass originated above the surface of the
ground and then grew underground, those of reed canarygrass
originated and grew underground (9).
Rhizomes can be distinguished from the aerial stems in that they have vestigial whitish scale leaves instead of the full-grown green leaves of the aerial stems. The transformation of rhizomes into aerial stems occurred through well-defined and easily distinguishable transitional forms. This gradual transition could be induced by changing the orientation of the shoot (20). Once this transition was complete, the orientation of the shoot could not cause the transformation of the aerial stems into rhizomes and vice versa, but in the earlier stages of this transition, the plant stem could be forced to go to the rhizomatous form or the aerial form of the shoot (20).

**Tissue organization in the aerial stems and rhizomes of grasses**

Very little work has been accomplished toward this aspect of the rhizomes of grasses. In the beginning of this century, the vascular tissues of the aerial stems of grasses were compared with those of rhizomes. It was found that the number of amphivasal vascular bundles in the rhizomes and the aerial stems of the same species was the same (4).

In order to distinguish the rhizomes (underground horizontal stems) and the stolons (above ground horizontal stems), Holm (14) studied the structure of these stems. He concluded that the rhizomes had the same structure as the main axis on which they were borne; the stolons on the other hand were different in structure from the stem on which they were borne. He did not indicate the structures which were different in stolons.
Efforts also were made to determine the factors affecting the rhizome formation. A study of the naturally growing grasses belonging to the genus *Muhlenburgia* was undertaken. It was found that while the species having rhizomes were all tetraploid, those without rhizomes were all diploid (21). The maturation or the ultimate drying of the main shoot appeared to be responsible for the rhizome formation in the grasses (12).

The morphology of the aerial shoots and the rhizomes of grasses were studied at The Ohio State University by Stover (33). He found a thick-walled, lignified and continuous pericycle around the vascular tissues of the rhizomes. This pericycle was present around each vascular bundle in aerial stems, but was not present in the interfascicular tissue or the tissue between the vascular bundles. The endodermis was also present in the rhizomes of grasses studied, while it was absent in the aerial stems. In the rhizomes a ring of tissue surrounded the vascular system and was situated outside the thickened and lignified pericycle. This endodermis gradually disappeared in the rhizome as it became aerial. The epidermis and the hypodermis in the stems of grasses became thick walled and lignified (33).

In the nodes of rhizomes as well as the aerial stems of grasses, amphivasal vascular bundles were found. The vascular bundles in aerial stems and rhizomes of *Agropyron repens* were found to be arranged in a single circle (34). Prat (25) had found earlier that 1-3 circles of vascular bundles were present in the stem of *Agropyron repens*.
The structure of rhizomes and culms (or grass stems) was found to be the same by Metcalfe (19) in his comprehensive treatise on the *Anatomy of Monocotyledons, I. Gramineae*. He found, however, that the rhizomes had well-developed sclerenchyma tissue. He also found that starch and other foods may accumulate in the ground tissues of rhizomes.

**Origin of rhizomes**

Rhizomes are defined as underground stems having some variation in structure from the aerial stems. The origin of the rhizome is, therefore, the same as the origin of an underground branch. The branches in aerial stems as well as in underground stems were seen to arise from the axillary buds on the stem. The divisions initiating an axillary bud (in aerial stems) occurred on the axis slightly above the point where the underlying leaf was found to be inserted. The subsequent growth of the axillary bud was brought about by periclinal divisions (9).

In *Agropyron repens*, no periclinal divisions occurred in either the dermatogen or the hypodermis at the position of the future bud, these two layers in the bud being continuous in the main axis and in the bud. The subhypodermis and core of the bud were found to be a result of the periclinal divisions in the sub-hypodermal layer of the main axis. This was seen to be true in the aerial stems and the rhizomes of *Agropyron repens* (30).
Shoot tip organization

The organization of the shoot apex was first conceived by Wolff (35). He considered the shoot apex as an undeveloped part of the plant responsible for its growth. The first study of the shoot apex of angiosperms was done by Hanstein (13). He concluded that the shoot apices, like root apices, consisted of several histogens, or a group of meristematic initials which differentiated into definite tissues. Although this theory worked well for the root apices, it did not hold true for the shoot apices of the angiosperms.

The tunica-corpus concept of the shoot apex was developed in the early part of the twentieth century by Schmidt (27). According to that theory, the shoot apex consisted of a tunica or the outermost layer with cells dividing only anticlinally, thus perpetuating themselves and allowing for the growth of the underlying tissues but not adding to the lower layers. The rest of the tissues constituted the corpus or core. The cells of the corpus divided both anticlinally and periclinally. This region, therefore, perpetuated itself and added to the future growth of the apex.

Since Schmidt's work on the organization of the shoot apex, a lot of literature has been accumulated. Excellent reviews have been written on this topic by Popham (22), Esau (8), and Gifford (11) and others to elucidate the principles involved in isolated descriptions of the shoot apices of different plants. According to the classification of shoot apices given by Popham (22),
Pteridophytes belonged to types I, II, and III in which one or more initials at the apex divide in all directions giving rise to peripheral meristem and central meristem with no well-defined mantle region. Gymnosperms belonged to the types IV and V with frequent periclinal divisions in the surface layer giving rise to the surface meristem. Angiosperms belonged to the types VI and VII with a well-defined mantle layer having only the anticlinal divisions in the surface layer. Type VI is the _Opuntia_ type with a cambium-like zone of cells separating the central mother cells from the peripheral and central meristems. This cambium-like zone was absent in type VII or the usual angiosperm type which had sub-apical initials rather than the central mother cells. The shoot apex of type VII occurred in the angiosperms only. Several grasses and cereals like _Dactylis glomerata, Agropyron repens, Triticum vulgare, Avena sativa, Secale cereale_, and _Zea_ belong to that type of organization. In the small monocotyledons of the Gramineae family, the peripheral meristem and central meristem might be absent or indistinct (22).

The rhizome apex of herbage grasses, according to Sharman (29, 32), was of intermediate type possessing 5-10 leaf primordia. The shoot tips of grasses were conical or dome shaped, a fraction of a millimeter long and consisted of 1-3 rudimentary phytomer ears below the undifferentiated apical meristem (10). It had large, vacuolated cells at the extreme tip which divided only anticlinally. Both the hypodermis and the subhypodermis were of
one-cell thickness, and formed concentric shells clothing a core of more vacuolated resting cells called apical pith (31).

The shoot apex of *Agropyron repens* consists of three layers, the dermatogen, the hypodermis, and the subhypodermis, enclosing a central core. The dermatogen and the hypodermis divided only anticlinally except at the position of the leaf primordia where they also divided periclinally. The subhypodermis might divide both anticlinally and periclinally (31).

Two tunica layers were found in the shoot apex of Festucoidae (to which tall fescue and bluegrass belong), while there was only one tunica layer in Panicoidae (2).

The type of shoot apex was not related according to Sharman (32) to the annual or perennial habit, nor was it related to the morphology of the stem (22). Palmer (20), however, felt that there might have been some observable changes in the shoot apex when the rhizome form of the stem was converted to the aerial form.

In the drawings presented by Sharman (30), without giving specific comment, the present reviewer believed that there is no difference between the shoot apices of the aerial shoot and the rhizome.
MATERIALS AND METHODS

Tall fescue plants were selected from The Ohio State University Farm where the "Alta" variety had been planted 3-4 years earlier. It was also collected, especially the rhizomatous plants, from the interstate highway, I-71 right of way about 25 miles north of Columbus, Ohio. At this location the "Alta" variety of tall fescue had been seeded along with Kentucky bluegrass, redtop (Agrostis alba L.) and alsike clover (Trifolium hybridum) in 1959-1960. Kentucky bluegrass and quackgrass were collected from around The Ohio State University gardens.

The specimens of stems thus collected were cut into pieces, about 5 mm long. These pieces were killed by Nawaschin's Solution, consisting of equal parts of freshly mixed Nawaschin A solution and Nawaschin B solutions. Evacuation of air from the rhizome pieces, by means of a faucet aspirator, was started immediately upon being placed in the fixing agent and continued for 24 hours. The rhizome pieces were then washed with running tap water for 4-5 hours. They were then dehydrated using 5%, 10%, 20%, 30%, 50%, 70%, 80%, 95%, and 100% dilutions of ethyl alcohol. They were left in alcohol for 4-5 hours up to 50% and overnight for the rest of the dilutions. They were left in absolute ethyl alcohol for 48 hours with 2-3 changes. The ethyl alcohol was then removed from the tissues by using graded series of absolute
ethyl alcohol and xylene mixtures. The tissues were left in these series for four hours in each mixture. Erythrocynin was put in the last mixture of alcohol and xylene so that the tissues could be distinguished from the paraffin in the ribbon. The tissues were left in xylene for 48 hours with 2-3 changes. Long pieces of paraffin were put in the xylene containing tissues and left for 12 hours at room temperature. More liquid paraffin was put in the tubes and they were put in an oven at 54°C just above the melting point of paraffin. Liquid paraffin was changed 3-4 times after removing all the xylene-paraffin mixture. The tissues were then embedded in paraffin blocks and solidified.

The paraffin embedded rhizome pieces were sectioned at 10 microns on a rotary microtome. The ribbons thus obtained were affixed to the slides, using Haput's adhesive, on a 50°C hot plate. The sections were stained after removing the paraffin by xylene. The staining procedure used was Saffranine-aniline blue using Methyl cellosolve and clove oil as mordants.

The following modified Saffranin-Aniline blue schedule was employed for staining the sections:

<table>
<thead>
<tr>
<th>Solution</th>
<th>Time</th>
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<tbody>
<tr>
<td>Xylene I</td>
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<tr>
<td>Xylene II</td>
<td>5 minutes</td>
</tr>
<tr>
<td>100% ethyl alcohol</td>
<td>5 minutes</td>
</tr>
<tr>
<td>95% &quot;</td>
<td>5 minutes</td>
</tr>
<tr>
<td>80% &quot;</td>
<td>5 minutes</td>
</tr>
<tr>
<td>70% &quot;</td>
<td>5 minutes</td>
</tr>
<tr>
<td>50% &quot;</td>
<td>5 minutes</td>
</tr>
</tbody>
</table>
Saffranin "0" 5 dips
50% ethyl alcohol 5 minutes
70% " " 5 minutes
80% " " 5 minutes
95% " " 5 minutes
100% " " 5 minutes
Methyl cellosolve 5 minutes
Clove oil 5 minutes
Aniline blue 15 minutes
90% alcohol + 10% xylene 5 dips
Xylene II 5 minutes
Xylene III 5 minutes

The sections were then mounted in piccolyte and used for the study. The photomicrographs were taken through a Bell and Howell research microscope having apochromatic objectives and a low ampliplan compensating photographic eyepiece for flatter image. A Gamma 4X5 bellows camera with a 120 film adapter was used for taking photographs on Kodak Panatomic X roll film. The films were developed using Microdol X developer diluted 1:3 and fixed in acid bath. The negatives were printed on RB 3 printing paper of the Fotorite rapid printing process in their special printing machine.
RESULTS OF THE STUDY

1. Tissue organization in aerial stems and rhizomes

Aerial stems of *Agropyron repens*, quackgrass

The tissue organization in aerial stems of quackgrass can be easily observed in the transverse section (Fig. 1). The outermost layer in the mature aerial stem is the epidermis. It consists of elongated, thickened cells. The thickening is non-uniform and is in the form of an inverted U. A layer of cuticle can be seen on the outside of the epidermis (Fig. 1).

Below the epidermis, the hypodermis can be seen. It consists of 3-5 layers of hexagonal, uniformly thickened cells. Under this tissue lies the ground tissue or the pith, of 10-15 layers of thin walled, rounded cells. The vascular tissue system is embedded in the hypodermis tissue. The cells of the hypodermis resemble that of sclerenchyma, a tissue present in the other grasses and in the rhizomes of quackgrass (Fig. 1).

The vascular tissue system in the aerial stems of quackgrass consists of 1-3 rings of collateral vascular bundles. Each vascular bundle consists of 3-4 large, thickened and lignified metaxylem vessels arranged in the form of Y and small phloem cells arranged as a circular patch. The phloem consists of the larger sieve tubes and the smaller companion cells. Each vascular bundle
Fig. 1.—T.S. of aerial stem of *Agropyron repens*, quackgrass. (x280)
is surrounded by a bundle sheath of uniformly thickened sclerenchyma. The sclerenchyma is continuous from one vascular bundle to the other in the outer ring of the vascular bundles but is not continuous in the inner ring of the vascular bundles. There is a lysigenous cavity in the center of the stem. This cavity is, perhaps, formed by the shrinkage of the inner layers of the ground tissue (Fig. 1).

**Rhizome of Agropyron repens, quackgrass**

The structure of the quackgrass rhizome in transverse section appears to be similar to the root rather than the aerial stems (Fig. 2). Like that in the root, the rhizome consists of an epidermis, a hypodermis, a well-defined cortical parenchyma, the endodermis, and the central cylinder or the stele. The arrangement of the vascular tissues in the vascular bundles, however, is like that in the stem.

The epidermis is the outermost layer of cells with the U-shaped thickenings. The hypodermis consists of 2-3 layers of uniformly thickened hexagonal cells. The cortical parenchyma consists of 10-12 layers of thin-walled, rounded cells with small air spaces between them (Fig. 3). The innermost layer of the cortex consists of a layer of lignified and suberised cells with U-shaped concentric thickenings. This layer, much like that found in the roots, is called the endodermis (Fig. 4).

The vascular system in the rhizomes of quackgrass consists of 1-2 rings of collateral bundles embedded in a uniformly
Fig. 2.—T.S. of the rhizome of *Agropyron repens*, quackgrass. (x87)
Fig. 3.—T.S. of the rhizome of *Agropyron repens*, quackgrass, to show the epidermis, hypodermis, and endodermis. (x163)
Fig. 4.--T.S. of the rhizome of *Agropyron repens*, quackgrass, to show the endodermis, sclerenchyma, and vascular bundles. (x150)
thickened sclerenchyma (or pericycle). The vascular bundle sheath is composed of sclerenchymatous cells. This sclerenchyma is continuous between the first as well as the second ring of the vascular bundles (Fig. 4). Each vascular bundle consists of three large metaxylem vessels and 1-2 small protoxylem vessels. The lysigenous cavities in vascular bundles are not as evident as in the aerial stems. The phloem tissue consists of larger sieve tubes and smaller companion cells.

There is a pith in the center of the stem and it is this pith of the rhizome which shrinks up to give a lysigenous cavity (Fig. 2).

The structure of the rhizome, therefore, resembles that of the roots in the presence of the cortex, endodermis and the pith. It resembles that of the stem in the arrangement of the vascular tissue system, i.e., the presence of xylem and phloem in the same radius instead of the different radii as found in the roots.

The following symbols were used in the labeling of the illustrations:

- Epidermis EPI
- Hypodermis HYP
- Cortical Parenchyma CP
- Endodermis END
- Ground Tissue or pith GT
- Pericycle PER
- Sclerenchyma SCL
- Phloem PHL
<table>
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<th>Term</th>
<th>Abbreviation</th>
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<tr>
<td>Sieve Tube</td>
<td>ST</td>
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<tr>
<td>Companion Cell</td>
<td>CC</td>
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<tr>
<td>Metaxylem</td>
<td>MX</td>
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<td>Protoxylem</td>
<td>PX</td>
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<tr>
<td>Lysigenous Cavity</td>
<td>LC</td>
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<td>Vascular Bundle</td>
<td>VB</td>
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<tr>
<td>Bundle Sheath</td>
<td>BS</td>
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<tr>
<td>Mantle</td>
<td>M</td>
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<tr>
<td>Sub-apical initials</td>
<td>SA</td>
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<tr>
<td>Central Meristem</td>
<td>CM</td>
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<tr>
<td>Peripheral Meristem</td>
<td>P</td>
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<tr>
<td>Corpus or Core</td>
<td>COR</td>
</tr>
<tr>
<td>Leaf Primordium</td>
<td>LP</td>
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**Aerial stem of *Poa pratensis*, Kentucky bluegrass**

The tissue organization in the aerial stems of Kentucky bluegrass can be easily observed in the transverse section (Fig. 5). The outermost layer of the stem is the epidermis. It consists of thin-walled, radially elongated cells.

Below the epidermis lies the ground tissue or the pith. The ground tissue consists of thin-walled, rounded cells with small air spaces between them. This tissue cannot be differentiated into the hypodermis, the cortical parenchyma and the endodermis. This is because of the fact that the cells of this tissue are all alike. There are no thickenings like those found in the hypodermis of
Fig. 5.—T.S. of the aerial stem of *Poa pratensis*, Kentucky bluegrass. (x346)
quackgrass or in the endodermis of the rhizomes of the grasses. No casparian dots can be observed.

The ground tissue is interrupted by a ring of the cells of the parenchyma tissue (Fig. 5). These cells are hexagonal in shape and have uniform thickenings formed by the deposition of lignin and suberin. The ring of sclerenchyma splits off 4-6 layers of cells resembling the cortex on the outside and 5-7 layers of cells resembling the pith on the inside. This sclerenchyma ring itself consists of 1-2 layers of cells. In this tissue, the vascular tissue system of the aerial stem of Kentucky blue-grass is embedded.

The vascular tissue system of the aerial stem consists of two rings of collateral vascular bundles. Each vascular bundle is enclosed in a bundle sheath which is endodermoid in nature. The bundle sheaths of two adjoining vascular bundles is joined together by the sclerenchyma.

The xylem and the phloem are arranged in the vascular bundles. The vascular bundles consist of two or three large metaxylem vessels arranged in the form of Y. The protoxylem vessels are sometimes present but their number varies with the vascular bundles in the same stem and is not constant for a species. It may be absent in some of the vascular bundles of the stem.

The phloem is arranged in the form of a circular patch. It consists of sieve tubes and companion cells. The cells of these two categories of phloem may be almost equal in size.
The inner ground tissue, lying in the center of the stem, consists of large thin-walled cells. These cells are similar to those outside the sclerenchyma ring and both may be called the ground tissue because of the absence of a well-defined endodermis and the stele (Fig. 5).

**Rhizome of Poa pratensis, Kentucky bluegrass**

The outermost layer of the rhizome of the Kentucky bluegrass consists of the epidermis (Fig. 6). The cells of the epidermis are small rounded and thickened.

Next to the epidermis lies the cortex. It consists of 4-6 layers of large, rounded and thin-walled cells with small air spaces between them. The outermost layer of the cortex cannot be distinguished as hypodermis. The innermost layer of the cortex consists of rounded cells with U-shaped concentric thickenings. This layer may be called the endodermis.

A sclerenchyma ring, 5-7 cells thick, lies on the inside of the endodermis. This layer corresponds to the pericycle of Stover (30) or sclerenchyma of Metcalf (16). It consists of hexagonal, uniformly thickened cells with vascular bundles embedded in it. The bundle sheaths of the vascular bundles resemble the sclerenchyma and cannot be distinguished from it except at the part of the vascular bundle which is towards the center of the stem.

The vascular system consists of one ring of collateral vascular bundles. Each vascular bundle is composed of 2-3 large metaxylem vessels arranged in the form of Y in cross section. The
Fig. 6.—T.S. of the rhizome of *Poa pratensis*,
Kentucky bluegrass. (x470)
phloem area consists of large sieve tubes and small companion cells. The pith lies in the center of the stem and consists of thin-walled, hexagonal to rounded cells with small air spaces between them. The pith of the rhizome is very small as compared to the ground tissue of the aerial stems.

Aerial stem of *Festuca arundinacea*, tall fescue

The tissue organization of the aerial stems of tall fescue can be easily seen in the transverse section (Fig. 7).

The aerial stems consist of the epidermis, the ground tissue, and the vascular tissue system. A sclerenchyma ring is present in the ground tissue and the vascular tissue system is embedded in it.

The epidermis consists of small rounded cells with thickenings in the form of an inverted U. There is a thin cuticle layer on the outside of the epidermis.

Just below the epidermis lies the ground tissue or the pith. It consists of 14-18 layers of cells separated by sclerenchyma into the outer ground tissue and inner ground tissue. The outer part consists of 10-12 layers of cells which are rounded and thin-walled with small air spaces in between. The sub-epidermal layer and the layer just outside the sclerenchyma ring are similar to the rest of the tissue. These two layers cannot be distinguished as hypodermis and endodermis respectively. The layer just outside the sclerenchyma ring does not have either the casparian dots or the concentric U-shaped thickenings in the cells.
Fig. 7.—T.S. of the aerial stem of *Festuca arundinacea*, tall fescue. (x72)
A well-defined sclerenchyma ring is present in the ground tissue. This ring is 3-4 cells thick, the individual cells being hexagonal in shape and uniform in thickness.

The vascular bundles are of collateral type. There is a sclerenchymatous bundle sheath around each vascular bundle.

This bundle sheath is 1-2 cells thick. The boundary between the bundle sheath and the sclerenchyma ring is not distinct on the outer 3-4 layers but is distinct in the rest of the bundle.

The xylem consists of three large metaxylem vessels and 3-5 small protoxylem vessels. The larger metaxylem vessels are arranged in the form of Y in cross section. There is a circular patch of phloem tissue with distinct enucleate sieve tubes and small nucleate companion cells (Fig. 8).

Rhizome of Festuca arundinacea,
tall fescue

The rhizomes of tall fescue are very rarely seen in summer but they are sometimes found in the spring and fall seasons of the year on some plants under central Ohio conditions. The transverse section of the rhizome reveals the epidermis, the cortex, the sclerenchyma ring, the vascular tissues, and the pith (Fig. 9).

The epidermis consists of small rounded cells with U-shaped thickenings, the thin side of each cell being on the inside of each stem. The cuticle cannot be easily seen on the outside of the epidermis.
Fig. 8.—T.S. of the aerial stem of Festuca arundinacea enlarged to show the details of the vascular bundles. (x400)
Fig. 9.—T.S. of the rhizome of Festuca arundinacea, tall fescue. (x192)
The cortex of the tall fescue rhizome consists of 14-16 layers of rounded cells. The outermost layer cannot be distinguished as hypodermis. The cortical parenchyma consists of thin-walled rounded cells with small air spaces between them.

The layer next to cortical parenchyma on the inside resembles it but has U-shaped concentric thickenings. This layer may be called endodermis because of its characteristic position and thickening. The endodermis in the rhizome of tall fescue may be 3-4 layers thick. It lies on the outside of the sclerenchyma ring. This sclerenchyma ring has been referred to as the pericycle (Stover, 30). The cells of the endodermis are rounded with U-shaped concentric thickenings; the cells of sclerenchyma are hexagonal with uniform lignification and thickening of all the cells in the tissue.

The sclerenchyma ring lies below the endodermis and consists of 3-5 layers of cells in which the outer ring of the vascular bundles is embedded. It is supposed to be the supporting tissue of the stem. When the pith of the rhizome starts breaking up and its cells shrink, the vascular bundles in the sclerenchyma ring can still be seen intact.

The vascular system of the rhizome of tall fescue consists of 2-3 rings of collateral vascular bundles embedded in sclerenchyma. Each vascular bundle consists of a bundle sheath of 2-3 layers of sclerenchymatous cells; 3-4 large metaxylem vessels arranged in the form of Y in cross section, and the protoxylem and lacunae are present in some of the vascular bundles. The phloem
is present in the form of a round patch and consists of large well-defined enucleate sieve tubes and the small nucleate companion cells (Fig. 9).

In the center of the rhizome is the pith which consists of rounded thin-walled cells resembling the cells of the cortex. The pith in the rhizomes of tall fescue is almost equal to the internal pith of the aerial stems.

2. Origin of rhizomes of *Festuca arundinacea*

In order to find out the origin of rhizomes, rhizomatous plants were selected from old stands of tall fescue turf. The underground part of tall fescue plant consists of two alternate rows of buds in the axils of scale leaves. This portion of the stem gives rise to the shoots of tall fescue. Some buds break dormancy and become underground shoots and others develop into aerial shoots. It was felt that it is not possible to ascertain beforehand which buds will give rise to rhizomes and which will give rise to aerial stems. It was, therefore, decided to find out the origin of the rhizomes from the development of the bud onwards, i.e., the layers in the bud which give rise to rhizomes, tracing it back from the well-developed rhizome.

For this purpose, serial transverse sections of the rhizome with buds and scale leaves were cut. Figure 10 shows the transverse section of rhizome with the earlier stage of rhizome development from the bud. It can be seen in this picture that the rhizome originated from the outer layers of the undifferentiated
Fig. 10.—T.S. of the rhizome of Festuca arundinacea, tall fescue, enlarged to show the origin of the rhizome. (x170)
cortex of the young stem. This is due to the presence of stacks of cells coming from the part of the cortex well above the endodermis (Fig. 10).

3. Shoot apex organization of aerial stems and rhizomes

Aerial stem of *Agropyron repens*, quackgrass

The aerial stem apex of quackgrass is a dome-shaped structure. At the point of the formation of the youngest leaf primordium it is about 84 microns high and 112 microns wide. A median longitudinal section through the stem apex reveals its organization (Fig. 11).

Clothing the shoot apex of aerial stem of quackgrass is a mantle zone consisting of two layers of cells. The outermost layer consists of cells dividing anticlinally only; except at the point of the formation of new leaf primordia where cells may divide both anticlinally and periclinally. In this respect, the outer layer of the mantle may be compared with the tunica, as reported by Schmidt (23a), without it having any relation to the histogenic nature of the tunica. The cells of the second layer of the mantle divide primarily anticlinally but a few periclinal divisions may be observed in this layer. The first and the second layers of the mantle correspond to the dermatogen and the hypodermis respectively as reported by Sherman (25).

The layers of cells under the mantle layer cannot be distinguished into the sub-apical initials, peripheral meristem and the central meristem, according to type VII or general angiosperm
Fig. 11.—L.S. of the aerial shoot apex of Agropyron repens, quackgrass. (x400)
type of shoot apex. The sub-mantle region can be called the corpus or core because there appear to be both periclinal divisions, anticlinal division, as well as slanting divisions in this region. The outer layer of the corpus can be compared to the sub-hypodermis as reported by Sharman (25), but this layer may consist of two cells at several places where the division has taken place. The region inside this layer or layers may be called the apical pith, having large cells. This corresponds to Popham's central meristem region. The periclinal division in the outermost layer, as seen in the photomicrograph, is at the youngest leaf primordium.

Rhizome of *Agropyron repens*, quackgrass

The rhizome apex of quackgrass is a dome-shaped structure. At the point of the formation of the youngest leaf primordium, it is about 88 microns high and 102 microns wide. A median longitudinal section through the stem apex reveals its organization (Fig. 12).

The outermost layer of the rhizome apex is the tunica layer, according to the tunica-corpus concept of shoot apex organization. The cells of this layer divide anticlinally only. This layer also may be referred to as the first layer \( (L_1) \) of the mantle, according to the mantle-core concept. The next layer of the mantle (hypodermis) consists of cells dividing mostly anticlinally. The cells of this layer near the tip are larger with many nucleoli.
Fig. 12.—L.S. of the rhizome apex of Agropyron repens, quackgrass. (x400)
The subhypodermis or the corpus region consists of a mass of cells dividing irregularly. Unlike the aerial stem the subhypodermis cannot be distinguished into a layer or two layers with most cells of one layer dividing into two. The apical pith or central meristem can be distinguished in this corpus. It is much clearer just below the first primordium.

The young leaf primordium can be easily seen with the periclinal divisions in the outermost layer in the mantle zone or the dermatogen.

Aerial stem of *Poa pratensis* L., Kentucky bluegrass

The aerial stem apex of Kentucky bluegrass is a dome-shaped structure. At the point of the formation of the youngest leaf primordium it is about 94 microns wide and 70 microns high. A median longitudinal section through the stem apex reveals its organization (Fig. 13).

On the outside of the shoot apex is a mantle zone or layer synonymous with the tunica layer because the cells in this layer divide only by anticlinal divisions. The cells of the mantle layer may divide anticlinally as well as periclinally at the point of the formation of the young leaf primordia.

Next to the single layered mantle on the apex lies a very small group of cells. This group of cells which divide both periclinally and anticlinally and which differ from the rest of the apex by their hexagonal to rounded shape may be referred to as the sub-apical initials.
Fig. 13.--L.S. of the aerial shoot apex of *Poa pratensis*, Kentucky bluegrass. (x256)
Just below the mantle layer and the region of sub-apical initials, two zones of cells can be distinguished. The long and narrow cells below the mantle form the peripheral meristem and the larger, rectangular cells in the center may be called the central meristem or apical pith (Popham, 22).

Rhizome of *Poa pratensis*, Kentucky bluegrass

The rhizome apex of Kentucky bluegrass is a dome-shaped structure. At the point of the formation of the youngest leaf primordia it is about 59 microns wide and 53 microns high. A median longitudinal section through the rhizome apex reveals its organization (Fig. 14).

The outermost layer of the rhizome apex consists of the mantle zone or the mantle layer. This layer also corresponds to the tunica because the cells undergo anticlinal divisions only. The cells of the tunica in the leaf primordial region may divide periclinally or anticlinally.

Next to the single layered mantle on the apex lies the region of sub-apical initials. These initials may consist of 2–3 large cells which appear to be separated from the rest of the meristems in the apex.

A peripheral meristem lies on two sides of and below the sub-apical initials. These cells are narrow and stain with more difficulty than the cells in the center of the shoot apex. These large cells in the center of the apex are hexagonal in shape and constitute the central meristem or the apical pith.
Fig. 14.—L.S. of the rhizome apex of *Poa pratensis*, Kentucky bluegrass. (x540)
Aerial stem of *Festuca arundinacea*,
tall fescue

The aerial shoot apex of tall fescue is a dome-shaped structure. At the point of the youngest visible leaf primordium it is about 70 microns high and 98 microns wide. A medial longitudinal section through the shoot apex shows its organization (Fig. 15).

The mantle zone of the aerial stem of the tall fescue consists of one layer of cells enclosing the apex. The cells in this layer undergo anticlinal divisions only. This layer may, therefore, be called the tunica layer.

Just below the single layered mantle is a region of cells dividing in many directions. These cells give rise to a row of cells just below the tunica and a region of cells in the center of the apex. These cells may be called the sub-apical initials.

The cells lying just below the tunica and derived from the sub-apical initials constitute the peripheral meristem. The cells of the peripheral meristem not only propagate the cells of this layer but also add to the cells in the center of the apex.

The cells lying in the center of the shoot apex may be called the central meristem or apical pith. The cells in this region are larger in size and undergo relatively fewer divisions than the other zones of the shoot apex.
Fig. 15.—L.S. of the aerial shoot apex of Festuca arundinacea, tall fescue. (x400)
Rhizome of *Festuca arundinacea*,
tall fescue

The rhizome apex of tall fescue is a broadly dome-shaped structure. At the point of the youngest visible leaf primordium, it is about 105 microns high and 137 microns wide. A median longitudinal section through the shoot apex reveals its organization (Fig. 16).

The mantle zone of the rhizome of tall fescue clothes its shoot apex. It is a single layer of cells dividing anticlinally only. The cells in the mantle layer divide in the periclinal fashion only at the young leaf primordia. This layer corresponds to the tunica layer in the tunica corpus concept of the shoot apex put forward by Schmidt (27).

Just below the single layered mantle of the rhizome lies a region of cells dividing in all directions and forming a kind of arc at the apical side of the rhizome apex. These cells are referred to as the sub-apical initials. These groups of initials give rise to all the subsequent tissues lying below the shoot apex except the epidermis which may or may not be derived from this layer alone.

The sub-apical initials in the shoot apex give rise to two types of meristems; the peripheral meristem on the sides and just inside the mantle layer, and the central meristem lying in the center of the shoot apex. The cells of the peripheral meristem and the central meristem divide in all directions. The cells of the central meristem are larger and divide less rapidly than peripheral meristem and are sometimes referred to as the apical pith.
Fig. 16.--L.S. of the rhizome apex of *Festuca arundinacea*, tall fescue. (x480)
DISCUSSION OF RESULTS

Various definitions of rhizome have been proposed on the basis of geotropism and the morphological characteristics. Rhizomes have pale, whitish, vestigial, scale leaves as compared to the green, fully expanded leaves of the aerial stems of grasses (20). They usually have thick-walled epidermis and hypodermis (33). They have been reported to have amphivasal vascular bundles in the nodes (4) and in the internodes (34). The vascular bundles of rhizomes of quackgrass were found to be in a single ring (34) or 1-3 rings (25). A ring of uniformly thickened cells found in the stems of grasses has been called pericycle (33) or the sclerenchyma (19).

Tissue organization in aerial stems

The aerial stems of quackgrass, Kentucky bluegrass, and tall fescue have certain anatomical similarities and differences. These three grasses belong to the family Gramineae; while the quackgrass belongs to the order Hordeae, Kentucky bluegrass and tall fescue belong to the order Festucoideae.

The tissue organization of the aerial stems of quackgrass is, broadly speaking, similar to the typical grass stem, corn (Zea mays). All the tissues are primary in origin. There is no cambium and therefore no secondary growth. The growth in diameter
takes place mostly by the enlargement of the cells of the ground tissue. These grass stems, therefore, remain relatively small at maturity.

The primary structure of the aerial stem of these grasses consists of the dermal tissue system, the fundamental tissue system and the fascicular or vascular tissue systems. The dermal tissue system consists of the epidermis. The epidermii of quackgrass and tall fescue have inverted, U-shaped thickenings. These thickenings are absent in Kentucky bluegrass.

The fundamental tissue system consists of the ground tissue in which the vascular tissue system is embedded. The outermost layer of the ground tissue can be identified as hypodermis only in the quackgrass. The hypodermis cannot be easily discerned in Kentucky bluegrass and tall fescue. The cells of the hypodermis in quackgrass are thickened and sclerenchymatous; the outermost ring of vascular bundles is embedded in this tissue.

The ground tissue or pith in Kentucky bluegrass and tall fescue is divided into an external ground tissue and an internal ground tissue by a ring of sclerenchyma. This sclerenchyma, though resembling that found in rhizomes, cannot be termed as pericycle. The pericycle comprises the outermost tissue of the stele. The stele is the vascular cylinder inside the endodermis, the innermost layer of the cortex with Casparian dots or concentric U-shaped thickenings. In this case the endodermis is absent; the stele is, therefore, absent and this tissue should, therefore, be referred to as sclerenchyma as done by Metcalf (17).
This sclerenchyma or pericycle was absent in aerial stems of grasses studied by Stover (30). The vascular bundles are embedded in this sclerenchyma ring. In quackgrass the sclerenchyma ring is absent in the aerial stem and the vascular bundles are embedded in hypodermis. The sclerenchyma tissue may be small or large depending upon the species.

The vascular system of the three grasses consists of one or more rings of collateral vascular bundles. No amphivasal bundles, reported earlier (3, 30), were found in any of the three grasses. The number of rings of vascular bundles was 1-3 in quackgrass, two in Kentucky bluegrass, and 1-2 in tall fescue.

Each vascular bundle has a bundle sheath around it. The xylem and phloem are arranged in a collateral fashion with phloem on the outside and xylem on the inside of the stem. The metaxylem vessels are found to be arranged in the form of "Y". Protoxylem may or may not be present and the number of protoxylem vessels varies among vascular bundles. The phloem consists of sieve tubes and companion cells. No amphivasal vascular bundles were found in the nodes or internodes of any of the stems of the grasses.

**Tissue organization in rhizomes**

The tissues in the rhizomes of grasses studied are arranged in a different manner than in the aerial stems. The epidermal of all rhizomes were thickened. Kentucky bluegrass rhizomes have uniform thickenings; quackgrass and tall fescue had U-shaped thickenings.
The fundamental tissue system consists of cortex. The outermost layers of cortex were identified as hypodermis only in quackgrass; the hypodermis was not discerned in Kentucky bluegrass or tall fescue.

The cortical parenchyma consists of varying layers of thin-walled rounded cells. It consisted of 10-12 layers in quackgrass, 5-7 layers in Kentucky bluegrass, and 14-16 layers in tall fescue.

The endodermis is present in the rhizomes of all the grasses studied. It consists of one layer in quackgrass, 2-3 layers in Kentucky bluegrass, and 3-4 layers in tall fescue.

The vascular system of rhizomes consists of varying rings of vascular bundles in a ring of sclerenchyma. Sclerenchyma consists of two layers in quackgrass, 3-5 layers in tall fescue, and 5-7 layers in Kentucky bluegrass. There are 1-2 rings of vascular bundles in quackgrass, one ring in Kentucky bluegrass, and 2-3 rings in tall fescue.

The vascular bundles in all rhizomes studied were of collateral type with varying number of layers in the bundle sheath: one in quackgrass, 1-2 in Kentucky bluegrass, and 2-3 in tall fescue. The xylem in the vascular bundles consists of 3-4 meta-xylem vessels arranged in the form of "Y". The protoxylem vessels may or may not be present and their number varies with the vascular bundle in the same section. The phloem consists of sieve tubes and companion cells. There is always pith in the center of the rhizomes.
Tissue organization of aerial stems compared with that of rhizomes

The rhizomes differ from aerial stems in the relative arrangement of the fundamental tissue system and the vascular tissue system. The vascular tissues in the aerial systems are embedded in the ground tissue. The rhizomes, on the other hand, have the vascular cylinder or stele embedded in the sclerenchyma ring. The sclerenchyma is a part of the vascular tissue system in rhizomes and is comparable to the pericycle; the sclerenchyma in aerial stems is a part of the fundamental tissue system represented by ground tissue.

There is a well-defined endodermis in rhizomes. It consists of 1-3 layers of cells. There is no layer in aerial stems which can be identified as endodermis. The pith in the rhizomes is part of the vascular tissue system, while that in aerial stems is a part of the fundamental tissue system.

The sclerenchyma ring is absent in aerial stems of quack-grass while it is present in rhizomes. There are two rings of vascular bundles in aerial stems of Kentucky bluegrass while there is only one such ring in its rhizomes.

There is no difference between the rhizomes and the aerial stems of grasses regarding the epidermis, type of vascular bundles, the number and arrangement of xylem vessels and the phloem tissues.
The origin of the rhizomes

The divisions on the shoot apex just above the leaf primordia initiate the axillary bud (8). The cells of the sub-hypodermis of the main axis undergo periclinal divisions resulting in the formation of the subhypodermis and the core of the bud (30).

The shoot apex of the tall fescue stem consists of a single layered mantle or tunica. The cells of this layer divide only antically and therefore cannot be responsible for the formation of the axillary bud and later the rhizome.

There are many transitional forms between the aerial stem and the rhizome. When the physiological conditions are conducive to the formation of the aerial stem, the rhizome may be converted into the aerial shoot. The origin of the axillary bud on the shoot apex, therefore, cannot be used to determine the origin of the rhizome. It is therefore necessary to determine the origin by cutting the transverse sections of the stems with rhizomes to arrive at the conclusion regarding the rhizome origin.

Serial transverse sections of tall fescue stems with rhizomes revealed that the layers of undifferentiated cortical parenchyma are responsible for the origin of the rhizomes, the hypodermis being absent in the rhizomes of tall fescue.

Shoot apex organization of grasses

The shoot apex organization, according to Sharman (28) is not related to the annual or perennial habit or the morphology of the stem. Palmer (20), however, thought that rhizomes might
show some observable changes when they are converted into aerial stems or vice versa.

The shoot apex organization of grass stems, according to Popham (22), belongs to type VII of his classification. According to this classification, the shoot apex consists of various zones, the mantle, the sub-apical initials, the central meristem, and the peripheral meristem. It has been reported that both Festucaoidae and Agropyron have a two-layered tunica (2, 22, 30). No difference between the shoot apex organization of aerial stems and rhizomes could be found in the drawings of Sharman (30).

A study of the shoot apices of the aerial stems and the rhizomes of quackgrass, Kentucky bluegrass, and tall fescue did not reveal any differences between the aerial stems and rhizomes.

The shoot apices of the three grasses studied showed type VII of the shoot tip organization. While there are two mantle layers in quackgrass stem, Kentucky bluegrass, and tall fescue have only one mantle layer.

The part of the shoot apex below the mantle zone in Agropyron is undifferentiated and can be called the corpus or core with central meristem apparent at the lower part of the apex. In this way it differs from the type VII of shoot apices.

Next to the mantle in the Kentucky bluegrass and tall fescue, the corpus can be distinguished into the sub-apical initials, the peripheral meristem, and the central meristem or the apical pith.
The mantle zone consists of cells which divide in anticlinal manner only. Very few periclinal divisions may be seen in the mantle zone. The sub-apical initials consist of cells which divide actively and in all directions. The peripheral meristem lies under the mantle zone and the cells in this zone also divide actively and in all directions. The central meristem lies in the center of the shoot apex and just below the sub-apical initials. The cells of this zone do not divide very actively but do divide in all directions.
SUMMARY AND CONCLUSIONS

This study was initiated to determine (1) the basic characteristics distinguishing the rhizomes from the aerial stems, and (2) the origin of tall fescue (*Festuca arundinacea*) rhizomes. Two well known rhizomatous grasses, Kentucky bluegrass (*Poa pratensis*) and quackgrass (*Agropyron repens*), were compared with tall fescue, a grass bearing rhizomes on rare occasions.

Transverse sections were used to study the tissue organization and median longitudinal sections to study the shoot apex organization of aerial stems and rhizomes. Serial transverse sections of the underground parts of tall fescue stems with rhizomes were used to study the origin of rhizomes.

All aerial stems had (1) the epidermis, (2) the ground tissue, (3) the collateral vascular bundles embedded in rings in ground tissue, and (4) the metaxylem arranged in the form of "Y" in cross section. The hypodermis was present only in quackgrass but was absent in tall fescue and Kentucky bluegrass. Sclerenchyma was present in tall fescue and Kentucky bluegrass but absent in quackgrass (Figs. 1, 5, 7, 8).

All rhizomes had (1) the epidermis, (2) the cortex with well defined endodermis, (3) sclerenchyma ring or pericycle, (4) collateral vascular bundles with metaxylem in the form of "Y" in cross section, and (5) pith in the center (Figs. 2, 3, 4, 6, 9, 10).
The relative arrangement of fundamental tissue systems and the vascular tissue system was different in rhizomes than that of aerial stems. All aerial stems had an undifferentiated fundamental tissue system with vascular bundles embedded in it. In rhizomes it was differentiated into the cortex with well-developed endodermis encircling the vascular cylinder. The sclerenchyma ring was present in both aerial stems and rhizomes except in aerial stems of quackgrass. The vascular bundles were embedded in this tissue except in aerial stems of quackgrass in which they were embedded in the hypodermis. The sclerenchyma is a part of the ground tissue in aerial stems, and of the vascular tissue (pericycle) in rhizomes.

Serial transverse sections of tall fescue stems with rhizomes revealed that the rhizomes are originated from the undifferentiated cortical parenchyma of the stem (Fig. 10).

The shoot apex organization of Kentucky bluegrass and tall fescue was similar to that described for type VII by Popham (20). In these apices, there was only one mantle layer over the sub-apical initials, the peripheral meristem and the central meristem. In the shoot apex of quackgrass, two mantle layers clothed an undifferentiated core. No fundamental differences between the shoot apex organization of the aerial stems and the rhizomes were observable in any of the grass apices studied.
BIBLIOGRAPHY


