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SCHAFFNERIA, A NEW GENUS OF GROUND DWELLING PLANT BUGS (HEMIPTERA, MIRIDAE)

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ABSTRACT. New genus *Schaffneria* is described to include three new species and two old ones from other genera. New species are *Schaffneria schaffneri* from Texas; *S. hungerfordi* from Michigan; *S. bureni* from Louisiana. *Pamillia davisi* Knight (1923) and *Ceratocapsus pilophoroides* Knight (1930) are transferred to *Schaffneria*. A key is provided for separation of the species.

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The genus *Schaffneria* includes at least five known species of ground dwelling plant bugs. Very few specimens have been collected during past years, and the writer believes this may be due to the strange habits of these bugs. Dr. Joe Schaffner and Dr. M.H. Sweet collecting in Texas, have found one species, *schaffneri*, living on the ground beneath cedar trees (*Juniperus virginiana* L.) where the bugs run about on ground litter, perhaps associating with ants. Dr. Sweet has observed these bugs probing or sucking juniper berries on the ground.

Schaffneria is related to *Pamillia* but may be separated as follows:

1. Apical area of corium frosted, pruinose, not polished; pronotal disk only slightly convex. . . . . *Pamillia* Uhler
   Apical area of corium and the cuneus, polished, strongly shining; basal half of pronotal disk strongly convex. . *Schaffneria* n. gen.

Schaffneria new genus

Allied to *Pamillia* Uhler but distinguished by having the cuneus, apical area of corium and embolium polished, strongly shining. Polished areas only sprasely set with pubescent hairs, a few longer hairs on paracuneus. Dorsal surface of hemelytra pruinose except on the polished areas; more strongly frosted in an irregular, transverse band behind scutellum; embolar margins more or less sinuate beginning at middle. Antennal segments strongly thickened as in *Pamillia* and *Ceratocapsus*, but species of *Schaffneria* may be distinguished from those genera by the highly polished areas. Arolia erect, apices converging which is typical of the Orthotylinae.

Type of genus: *Schaffneria schaffneri* new species.

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Key to species of Schaffneria

1. Width of vertex equal to more than half the width of head; antennal segment III slightly thicker than segment I. . . . davisi (Kngt.)
   Width of vertex equal to not over half the width of head; antennal segment III not thicker than segment I. 2

2. Wing membrane opaque white, not shaded darker. . . . . pilophoroides (Kngt.)
   Wing membrane white, but apical half shaded with fuscous to black. 3

3. Antennal segment III equal in thickness to segment I; lateral margin of embolium sharply sinuate. . . . . hungerfordi n. sp.
   Antennal segment III scarcely equal to thickness of setment I; lateral margin of embolium just slightly sinuate. 4

4. Prothorax, scutellum, polished apical area of corium and the cuneus, brownish black. . . . . schaffneri n. sp.
   Prothorax, scutellum, and hasal half of hemelytra yellowish, not infuscated; only the polished apical area of hemelytra and the cuneus, brownish black. . . . . bureni n. sp.

Schaffneria schaffneri new species

Distinguished from allied species as shown in the key.

Male. Length 2.8 mm. Head: width .78 mm, vertex .34 mm; color brown, lower face reddish brown, eyes darker brown. Basal edge of vertex sharp, extending back and above the narrow collar edge of pronotum. Antennae: segment I, length .31 mm, thickness .08 mm, pale yellowish brown, subtranslucent, with three bristles on anterior face; II, length 1.15 mm, slightly more slender on basal half, thickness on apical half .08 mm, or just equal to that of segment I, brown, clothed with very short, pallid pubescence; III, .74 mm, thickness .07 mm, slightly less than segment I, color uniformly medium brown, thickly clothed with very short, fine pale pubescence; IV, .58 mm, slightly more slender than III, tapering to apex, dark brown. Rostrum, length 1.26 mm, reaching upon apices of hind coxae, brown, reddish brown on first segment. Pronotum, length .61 mm, width at base .92 mm, lateral margins of disk concave in outline, more sharply curved on basal half; disk brownish black, moderately convex, impunctate, moderately shining, clothed with short, inconspicuous pale pubescence. Scutellum brownish black, apical half moderately convex, bearing four or five erect pubescent hairs, impunctate.

Hemelytra: width .98 mm across middle, flaring slightly to wider (1.05 mm) just before apex; dark brown to brownish black, a subtriangular pruinose area on middle of clavus, the pruinose area spreading to cover central area of corium, giving it a frosted aspect; apical area of corium and embolium, also the cuneus, shining to polished brownish black; clothed with very fine short pubescence, intermixed with a few, longer, suberect, golden brown hairs; membrane frosted, opaque, shaded with fuscous on veins and across middle, the color effect changing with angle of view.

Ventral surface brown to dark brown, venter shining, dark brown, ostiolar peritreme white; middle of venter and genital segment with longer, more prominent pubescence; genital claspers inconspicuous, left clasper slender, curved, acuminate on apical half, ending in a sharp point (Fig. 1). Legs rather uniformly dark brown, tibiae with double row of spines, length of spines about equal to diameter of tibia. Arolia erect, apices incurved, typical of Ceratocapsus and Pilophorus.

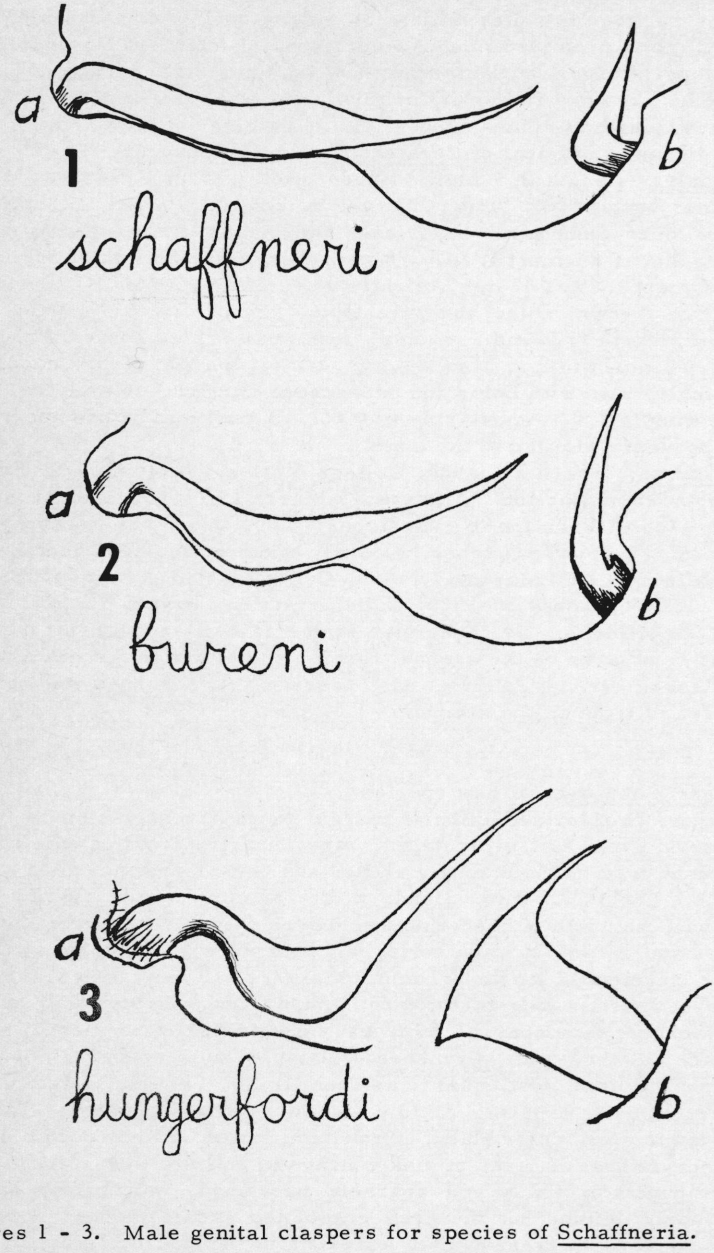
Female. Length 2.9 mm. Head: width .79 mm, vertex .37 mm. Antennae: segment I, length .31 mm, thickness .10 mm; II, 1.19 mm, slightly more slender on basal half, thickness .10 mm near apex, just equal to that of segment I; III, .76 mm, thickness .09 mm, slightly less than segment I; IV, .60 mm, slightly more slender than III, tapering to apex, dark brown; color and pubescence similar to that of the male. Rostrum, length 1.24 mm, reaching upon apex of hind coxae. Pronotum, length .64 mm, width at base .95 mm, lateral margin of disk concave as in the male, also with color and pubescence similar. Hemelytra: width across middle 1.02 mm, flaring wider (1.19 mm) just before apex; color and pubescence similar to the male.

Holotype: ♂ March 17, 1965, College Station, Texas (Joe C. Schaffner); author's collection. Allotype: ♀ March 19, 1965, taken at the type locality (Joe C. Schaffner). Paratypes: 6 ♂♂, taken with the type; 1♂1♀, March 29, 1965, 2♂1♀ October 19, 1963, taken at the type locality (Joe C. Schaffner). 2 ♂♂ March 17, 1965, College Station, Texas (Phil Wagner). 1♂2♀♀ October 8, 1965, College Station, Brazos County, Texas (Joe C. Schaffner). Dr. Schaffner states that all specimens including nymphs were taken on the ground, running and hiding in the litter beneath cedar trees. Dr. M.H. Sweet has observed that the bugs may feed on cedar fruits lying on the ground.

Schaffneria hungerfordi new species

Larger, broader and embolar margin more strongly sinuate than in schaffneri; basal half of scutellum rises sharply from middle, and is covered at base by the strongly arched and convex pronotal disk.

Male. Length 3.5 mm. Head: width .88 mm, vertex .38 mm which is not half the width of head; compound eyes do not rise above the level of frons and vertex, surface coriarious in texture, brownish black. Antennae: segment I, length .27 mm, thickness .10 mm, yellowish brown, with three bristles on anterior face; II, 1.05 mm, more slender on basal half, thickness near apex .10 mm, just equal to that of segment I, brownish black, clothed with very short yellowish pubescence; III, .65 mm, thickness .10 mm, just equal to segment II; IV, .61 mm, slightly more slender than III, tapering rapidly to apex, brownish black. Rostrum imbedded in glue, color black. Pronotum, length .85 mm, width at base 1.19 mm; lateral margins of disk concave in outline, disk strongly convex, impunctate, finely and sparsely pubescent, moderately shining; calli poorly defined but the area granulated and alutaceous, brownish black. Scutellum transversely wrinkled on apical half, apical area moderately convex, basal half steeply elevated, shining, covered above by the strongly arched pronotal disk which turns down sharply to cover base of scutellum, brownish black.



Figures 1 - 3. Male genital claspers for species of Schaffneria.

a. left clasper, posterior aspect
b. right clasper, posterior aspect

Hemelytra: width before middle 1.19 mm, embolar margin sinuate, flaring at middle to width of 1.42 mm near apex; brownish black, basal half and obliquely to tip of clavus, pruinose; behind that the apical area of corium, the embolium and cuneus, polished, shining; the pruinose area with minute short pubescence, intermixed with some minute sericeous, pubescent hairs, intermixed on basal half of corium with a few erect, bristle hairs; the polished area nearly black, sparsely set with rather short, more recumbent pubescent hairs. Membrane and veins brownish black, opaque, surface appears pruinose in some angles of light, somewhat paler near margins. Ventral surface brownish black, venter shining, ostiolar peritreme white. Legs brownish black, trochanters pale; tibiae nearly straight, with two rows of spines, length of spines not equal to diameter of tibia. Venter brownish black, shining, sides more polished; median ventral area with longer, more prominent pale pubescence; male claspers distinctive, left clasper curved, apical half slender, tapering to a sharp point; right clasper rectangular, apex terminating in a vertical sharp point above, and below in a shorter sharp point (Fig. 3).

Female. Length 3.6 mm. Head: width .92 mm, vertex .44 mm; form and surface texture similar to the male. Antennae: segment I, length .30 mm, thickness .10 mm, pale brownish; II, 1.05 mm, more slender on basal half, tapering to thicker (.10 mm) near apex; III, .64 mm, thickness equal to segment II; IV, .61 mm, slightly more slender than III, brownish black. Pronotum and hemelytra very similar to the male.

Holotype: ♂ July 14, 1931, Cheboygan County, Michigan (H. B. Hungerford); author's collection. Allotype: ♀, taken with the type.

We have held this species many years, hoping more material would turn up. Apparently, species of this genus are ground dwellers associated with ants, and so are seldom taken by collectors using nets in the usual manner. The species is named for the collector, my old friend Dr. H. B. Hungerford, long time Professor and Head of Entomology at Kansas University. He was a specialist and authority on aquatic Hemiptera. I knew him first as a graduate student at Cornell University (1916), and later when I was on the staff of the University of Minnesota, Dr. Riley brought him to Minnesota for summer work (1922). We spent a month collecting in northern Minnesota, seeking Hemiptera primarily, and Dr. Hungerford specializing on aquatic Hemiptera. For several years Dr. Hungerford spent part of each summer in northern Michigan, teaching entomology at the Douglas Lake Field Laboratory, operated by the University of Michigan. It was there he collected this rare bug which now is dedicated to honor his name.

Schaffneria bureni new species

Allied to schaffneri and distinguished as shown in the key.

Male. Length 3.3 mm. Head: width .78 mm, vertex .38 mm; form similar to schaffneri but color brownish yellow. Antennae: segment I, length .28 mm, thickness .10 mm, yellowish, with three small bristles on anterior face; II, 1.19 mm, more slender on basal half, thickness .09 mm near apex, yellowish brown, with very fine, short, pale pubescence; III, .75 mm, thickness .09 mm, yellowish brown; IV, missing. Rostrum, length 1.3 mm, reaching upon apex of hind coxae, yellowish, first two segments reddish. Pronotum, length .68 mm, width at base .98 mm; lateral margins of disk concave, forming a line uniform in curvature, disk strongly convex, impunctate, shining, bearing sparsely set pubescent hairs, calli not distinguished; color uniformly brownish yellow. Scutellum brownish yellow, apical half horizontal, moderately convex, basal half steeply elevated, covered above by posterior margin of pronotal disk; bearing a few sparsely set pubescent hairs.

Hemelytra: width 1.02 mm on basal half, embolar margin sinuate, flaring at middle to a width of 1.22 mm before apex; brownish yellow on basal half; apical half of clavus with fuscous, transversely pruinose behind scutellum; apical two-fifths of corium and embolium, and the cuneus, brownish black and polished; membrane and veins fuscous and opaque. Ventral surface yellowish to brownish yellow, ostiolar peritreme white, legs brownish yellow, tibiae darker; tibial spines yellowish, length of spines less than diameter of tibia. Venter brownish black, sides polished; pubescence longer beneath along middle. Genital claspers distinctive, right clasper angulate, apical half turned vertically, forming a sharp point (Fig. 2).

Holotype: ♂ June 8, 1943, Alexandria, Louisiana (Wm. F. Buren); author's collection. Named for the collector, Mr. Wm. F. Buren, who took his M.S. degree at Iowa State in 1942. His thesis was on the classification of Iowa ants, and published under the title "List of Iowa Ants (Formicidae)." During the war he was a member of a unit doing "Mosquito Control" work and stationed near Alexandria, La., when he collected the rare species here described.

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REACTIVATION OF THE DORMANT EMBRYO, AND INITIATION AND DEVELOPMENT OF BUDS AND LEAVES IN AVENA SATIVA[1]

G. J. Ikenberry, Jr.[2,3]

ABSTRACT. This study was undertaken to provide more information on the structure and development of the post-dormant vegetative phase of Avena sativa L. Twelve hours after imbibition, the radicle has penetrated the pericarp. Mitotic divisions occur by 24 hours in the radicle, and by 27 hours, figures are abundant in the radicle, seminal roots, coleoptile node, and first foliage leaf. Complete mitotic reactivation takes place by 36 hours. Each leaf is initiated by a periclinal division in the tunica. Both the tunica and the corpus contribute to the leaf primordium after the initiating divisions. The third foliage leaf is initiated within 45 hours. Nine foliage leaves are initiated before transition to the floral phase occurs, 10 days after emergence from the soil. An axillary bud is initiated be periclinal divisions in the corpus, in the acil of the second foliage leaf below the stem apex. The tunica of a bud is derived from the tunica of the main axis. Buds arise acropetally in the axils of the first 4 or 5 foliage leaves at intervals of 2 to 4 days. All buds undergo floral transition.

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Avena sativa L. has been the subject of numerous investigations. With a few exceptions, these studies have related to the improvement of the species as a crop plant. Our knowledge of the oat plant remains incomplete, particularly some aspects of its early development.

The present investigation was undertaken to provide more information on the post-dormant resumption of growth in the embryo, and initiation and development of leaves and buds.

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[1] Journal Paper No. J-5272 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project No. 1176. Received Dec. 12, 1965. Portion of a dissertation submitted to the Graduate Faculty of Iowa State University in partial fulfilment of the requirements for the degree Doctor of Philosophy.

[2] The author wishes to express his sincere appreciation to Dr. John E. Sass for his guidance during this investigation. Appreciation is also due Dr. K. J. Frey for providing field plots and seed used in the study. Gratitude is extended to the Quaker Oats Company for financial support during a portion of these investigations.

[3] Professor of Biology, McPherson College, McPherson, Kansas.

REVIEW OF PERTINENT LITERATURE

The structure of the dormant embryo of Avena has been described by Avery (1930). Avery and Burkholder (1936) investigated the structure and growth of the Avena coleoptile, and reported that cell division ceases by the time the coleoptile is one-fourth its mature length and that cell elongation is greater in the basal region. Holt (1955) described some features of the normal developmental histology of the oat seedling in relation to the response of plants treated with 2,4-dichlorophenoxyacetic acid. The normal seedling was found to have four leaf primordia at emergence from the soil.

The homologies in the embryo have been interpreted and reviewed adequately by Avery (1930), McCall (1934), and Boyd and Avery (1936). The more recent work by Boyd and Avery (1936), Reeder (1953), and Tucker (1957), strengthens the interpretations by Avery (1930) in which he states that: 1) the coleoptile is the first leaf above the single cotyledon, 2) the first internode (mesocotyl) extends from the cotyledonary node to the coleoptilar node, and 3) the epiblast is probably of little morphological significance.

Reviews of earlier studies on the shoot apex have been adequately presented by Foster (1941). Foster (1939, 1941) and Gifford (1954) have reviewed the comparative and developmental morphology of the shoot apex in seed plants. General descriptions and reviews of the developmental morphology of the grasses, with particular emphasis on the shoot apex, have been presented by Barnard (1957), Evans and Grover (1940), and Sharman (1942, 1947).

Sharman (1945, 1947) has described the shoot apex in Agropyron repens (L.) Beauv. as having three thimble-shaped layers, designated as dermatogen, hypodermis, and subhypodermis, all of which enclose a central core. He found that leaf primordia can first be detected by periclinal divisions in the dermatogen and that the young leaf is derived entirely from the dermatogen and hypodermis. He interpreted the dermatogen and hypodermis of axillary buds as being derived from the same layers of the main axis, whereas the subhypodermis and central core of the bud are derived from the subhypodermis of the main axis.

Abbe et al. (1941, 1951, 1951) found that the increase in size in the shoot apex of maize during successive plastochrons was due to an increase in cell number, the cell size remaining constant. They also found that the duration of successive plastochrons decreased markedly during the initiation of leaves 7 through 14.

Sharman (1942a) studied the developmental anatomy of the shoot of Zea mays L. He found that periclinal divisions in the dermatogen (protoderm) and underlying cells indicate the initiation of a leaf. He speculated that the marginal meristem of a leaf is concerned in the formation of the bud which appears later in the axil of the leaf below.

Kleim (1937) described the formation of leaf primordia in Avena sativa, designating everything inside the single tunica layer as the corpus, although he reported a hypodermis in older meristems. Predominantly anticlinal divisions were noted in the hypodermis, whereas those in subhypodermal region were largely periclinal. Kleim favored the concept that the corpus originates from one or two initials or groups of initials just beneath the tunica.

Hamilton (1948) compared the developmental anatomy of the shoot in four varieties of Avena grown at 16° C and 28° C. The "formative period" was found to extend over the first 3 weeks. She designated the regions in the apical meristem as dermatogen, hypodermis, subhypodermis, and core.

Bonnett (1961) has more recently reviewed and described the histology and development of the cultivated oat plant, Avena sativa.

MATERIALS AND METHODS

Two agronomic varieties of Avena sativa, Cherokee and Clintland, were used in these studies. Plants used in the study of imbibition, reactivation, and growth prior to emergence from the soil were grown at a constant temperature of 20° C. Collections were made at 3- and 6-hour intervals.

Plantings for field material were made on April 15, 1957, at the Iowa State Agronomy Farm. Seedlings emerged from the soil 8 days later. Grain was planted at the rate of 3 bushels per acre. Collections were made on alternate days throughout the growing season.

Since stages up to emergence from the soil were obtained from the germinator and later stages were obtained from the field, the designation "days after planting" is the sum of days required for emergence at 20° C plus the number of days after emergence in the field.

Tissues were fixed in Craf III (Nawaschin type) and processed for sectioning in parafiin by using dioxan-tertiary butyl alcohol or a modified ethyl alcohol-tertiary butyl alcohol series.

RESULTS

Dormant embryo—The dormant embryo of Avena lies near the base of the caryopsis, with the anterior side of the embryo adjacent to the aleurone and pericarp and with the posterior surface of the scutellum in contact with the endosperm. The embryonic shoot, encased in the coleoptile, has a short domed apex, subtended by two foliage leaf primordia. In cross-section, the first leaf completely encircles the apical meristem, whereas the second leaf is a small crescent. A minute bud primordium is located in the axil of the coleoptile.

The coleorhiza encloses and is contiguous with a well-developed radicle and root cap. The epiblast is a flattened structure that extends upwards from the anterior surface of the coleorhiza. There are two, rarely three, endogenous seminal roots extending laterally and downward from the level of the scutellar node.

Vascularization in the dormant embryo is represented by partially differentiated procambium strands. The scutellar node (scutellar plate) is a zone of anastomosing procambium immediately proximal to the immature stele of the radicle. In addition to the procambium extending from this point into the seminal roots, two main procambium strands extend toward the plumule. The large posterior strand bends sharply near the region of the coleoptile node, where it receives two strands from the coleoptile, then continues toward the tip of the scutellum where it branches into numerous strands (Fig. 1).

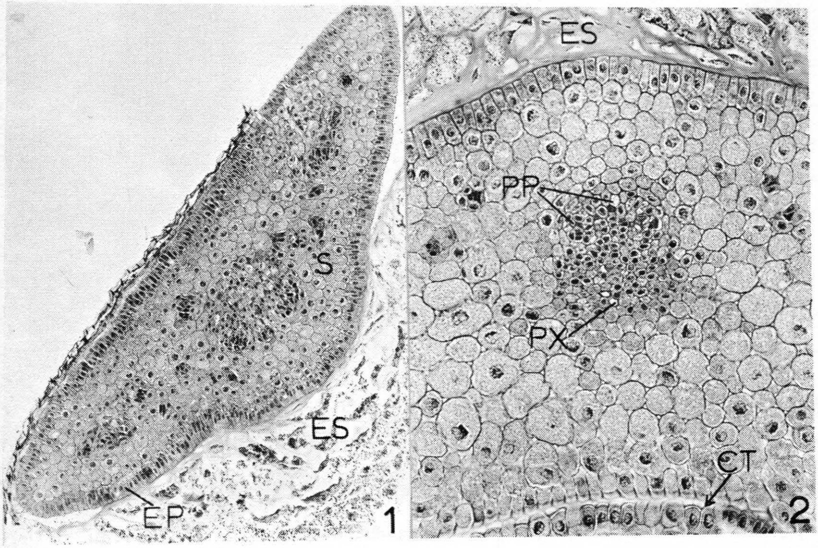


Figure 1. Cross-section through the distal portion of the scutellum in a dormant embryo. (X 50)

Figure 2. Cross-section of the procambium strand in the scutellum of the dormant embryo. The section is at the level of the stem apex. (X 100)

Scutellum	(S)
Endosperm	(ES)
Epithelial layer	(EP)
Protophloem	(PP)
Protoxylem	(PX)
Coleoptile	(CT)

The anterior strand extends to a level slightly above the coleoptile node, at which point it becomes continuous with the mid-procambium strand of the first leaf.

In transverse section the proximal region of the large central procambium strand of the scutellum has one or two annular or spiral protoxylem elements adaxially and two to five protophloem elements abaxially (Fig. 2). The first foliage leaf of the dormant embryo has 11 to 13 procambium strands which vary in size and stage of development. The large strand of the mid-rib has two to three protophloem elements and one differentiated protoxylem vessel. One protophloem element is evident in each of the two vascular strands which are located mid-way between the mid-vein and lateral edges of the first leaf. The coleoptile has one to two protophloem elements in the basal region of each of the two lateral provascular strands, but no protoxylem is evident at dormancy.

The first internode (mesocotyl) has one to three protoxylem and protophloem elements in each of the two main procambium strands, the anterior strand being larger and more highly differentiated. The stele of the radicle has seven or eight protophloem sieve tubes arranged circumferentially around a central, thin-walled, immature metaxylem element. Protoxylem is not evident although areas of its future development are distinguishable.

Germination—The first indication of reactivation and growth in the *Avena* embryo may be detected less than 12 hours after the beginning of imbibition. Enlargement of cells occurs in the coleorhiza and epiblast, as well as less pronounced cell enlargement in the region of the scutellar node and unexpanded mesocotyl. As a result of this enlargement, the coleorhiza and radicle rupture the pericarp before 12 hours. The cells of the root cap, radicle, and coleorhiza are contiguous at this stage (Fig. 3).

Subsequently, the radicle begins to elongate, but more rapid longitudinal expansion of the coleorhiza causes it to separate from the root cap (Fig. 4). The radicle penetrates the lemma by 24 hours. Continued enlargement in the coleorhiza causes complete separation from the primary root by 27 hours (Fig. 5).

Continued growth of the coleorhiza, epiblast, and scutellum is by cell enlargement only, since mitotic divisions have not been observed in these structures during germination. Fig. 6 indicates the regions of relatively greater cell enlargement at 36 hours. At this stage, the radicle has penetrated the coleorhiza.

By 60 hours, the epithelial cells of the expanding scutellum have undergone extensive radial elongation. Epidermal cells of the epiblast have given rise to numerous multicellular hairs at this stage.

Mitotic activity was found to occur by 24 hours after the dry kernels were placed in moist vermiculite in the germinator at 20 C. The first mitotic divisions were observed in the epidermis (protoderm) and cortex (periblem) of the radicle, some distance above the root histogens (Fig. 4). From this region, mitosis is initiated progressively toward the root apex, including the stele, root histogens, and calyptrogen.

By 27 hours, mitotic figures were abundant in the radicle, seminal roots, coleoptile node, and first leaf. Some mitotic activity is also present in the basal portion of the coleoptile and in the region of the

Figures 3-6. Projection drawings of the early stages of post-dormant growth in the Avena embryo axis. Small "x's" indicate the areas of mitotic activity. (X 17)

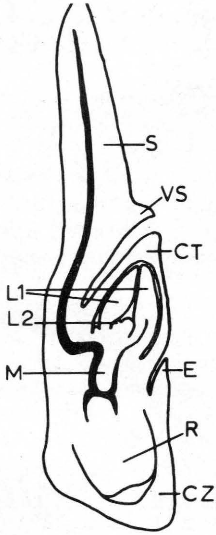
Fig. 3. The dormant embryo.

Fig. 4. The embryo 24 hours after imbibition has begun.

Fig. 5. The embryo axis 27 hours after imbibition has begun.

Fig. 6. The embryo axis 36 hours after imbibition has begun.

Scutellum	(S)
Ventral scale	(VS)
Coleoptile	(CT)
First foliage leaf	(L1)
Second foliage leaf	(L2)
Epiblast	(E)
First internode	(M)
Radicle	(R)
Coleorhiza	CZ)



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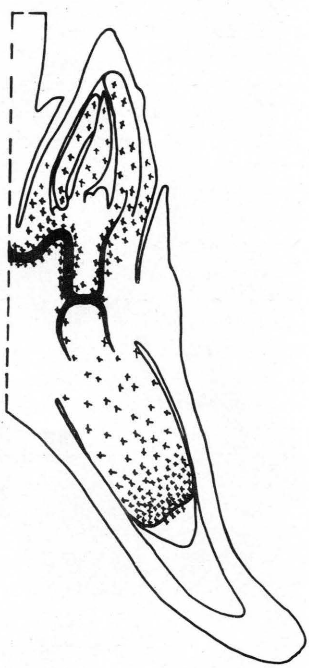
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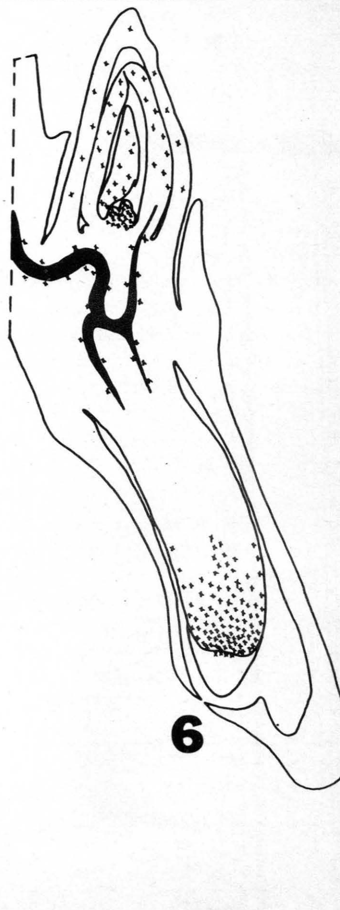
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mesocotyl and vascular arch (Fig. 5). The procambial cells of the various organs are particularly active. Nuclei of the shoot apex and second leaf are not yet dividing.

Mitotic figures can be found in the second leaf primordium and near the base of the apical dome at 30 hours.

Complete mitotic reactivation has occurred by 36 hours. Mitotic divisions are most numerous in the stem and root apical meristems, the second leaf primordium, and in the developing vascular strands (Fig. 6). Division figures are present, although somewhat less frequent, in the first leaf, particularly at the margins and in the procambium strands, and in the coleoptile.

Leaf initiation and ontogeny—The shoot apex of the embryo in the dormant Avena caryopsis is a short dome, subtended by the primordia of two foliage leaves. Longitudinal sections of the stem tip at this stage indicate differentiation into an outer single layer of cells, the tunica, and an inner zone of cells, the corpus. Periclinal cell division in the tunica indicates the initiation of the next leaf primordium, the third foliage leaf. This division occurs a short distance below the stem tip and may be detected in both transverse and longitudinal sections (Figs. 7, 8). Reference to foliage leaves by number in this study indicates their acropetal sequence of initiation.

From the zone of initiation, periclinal divisions spread laterally around the apex, accompanied by random divisions in the corpus, which together give rise to a crescent-shaped ridge that partially encircles the stem (Fig. 9). Further lateral spread of cell divisions results in the formation of a collar-like leaf base that completely surrounds the stem. This annular leaf primordium elongates by cell division in the meristematic margin, and the leaf soon arches over the apex. Successive loci of initiation occur directly opposite and above preceding ones, and thus initiate the two-ranked, distichous, arrangement of leaves.

Leaf initiation soon involves both tunica and corpus, hence some of the inner tissues of a leaf are derived from the surface layer, the tunica or protoderm. Intercalary growth at the leaf base gives rise to the tubular sheath. The ligule is derived from the adaxial surface layer, protoderm, of the leaf primordium, by periclinal cell divisions. The ligule is first detected on the third or fourth leaf from the stem tip at the level of the apex.

As the leaf primordium continues to expand, the meristematic lateral margins meet and then overlap. The edge of a leaf consists of a single row of cells, except in the distal region. The maximum thickness of the leaf in cell layers is attained approximately eight to 12 cells from the edge. Further increase in leaf thickness can be attributed largely to cell enlargement.

The third foliage leaf is initiated within 45 hours after the caryopsis has been placed under favorable conditions for germination. Initiation of the fourth leaf and morphological changes which occur in the shoot apex during the subsequent plastochron* are illustrated by the series of drawings in Figures 10 to 14.

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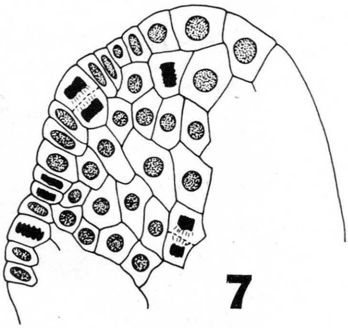
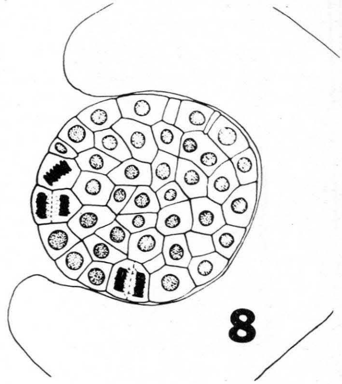
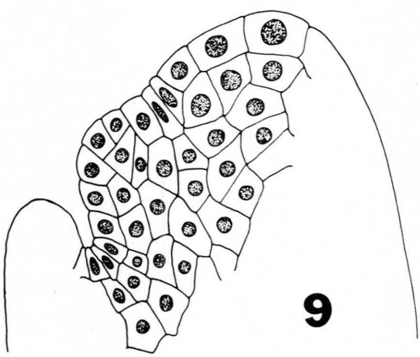
* A plastochron is the time interval between the initiation of successive leaf primordia.





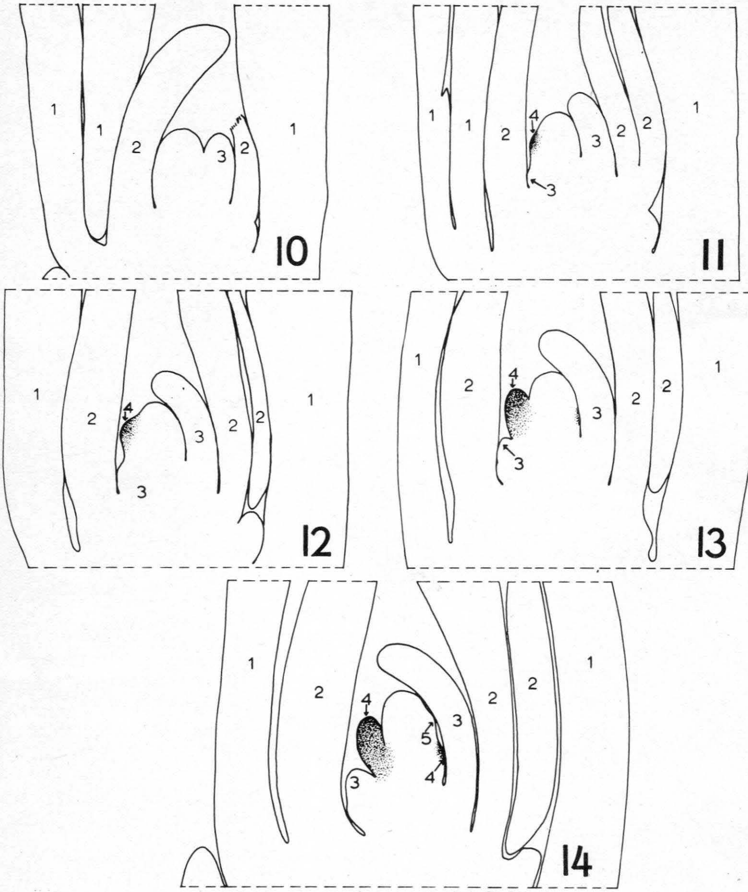


Figures 7-9. Projection drawings of the stem apex during the initiation of the fourth foliage leaf. (X 290)

Fig. 7. Longitudinal section of the stem apex showing a periclinal division in the tunica. (45 hours after imbibition)

Fig. 8. Transverse section of the stem apex showing a periclinal division in the tunica. (45 hours after imbibition)

Fig. 9. Longitudinal section of the stem apex showing a small leaf primordium which arises as a result of both periclinal and anticlinal divisions in the tunica. (60 hours after imbibition)



Figures 10-14. Series of drawings showing the changes which occur in the shoot apex during a plastochron involving the initiation of the fourth foliage leaf. Leaves are numbered according to their sequence of initiation. (X 240)

Fig. 10. Apex prior to initiation of fourth leaf. (84 hours after imbibition)

Fig. 11. Initiation of the fourth leaf. (120 hours after imbibition)

Fig. 12. Enlarging of the fourth leaf primordium. (126 hours after imbibition)

Fig. 13. Apex just prior to initiation of the fifth leaf. (144 hours after imbibition)

Fig. 14. Initiation of the fifth leaf. The fourth leaf has nearly encircled the shoot apex. (168 hours after imbibition)

Successive leaf primordia can be detected at intervals of 1 to 3 days prior to the formation of inflorescence primordia. There is a definite shortening of the plastochron as the axis approaches transition. This is associated with the gradual lengthening of the shoot apex during the initiation of the last three phytomers. Compare the vegetative apex in Fig. 15 with transitional apex in Fig. 16. Transition to the flowering phase and initiation of inflorescence branch primordia has occurred by 10 days after emergence. Table 1 indicates the time of initiation of the leaves and transition to the floral phase, and relates this to the external appearance of the plant.

Table 1. Organogeny of the main axis as related to time of initiation and external appearance of the plant.

Leaf number in order of initiation	Time of initiation or occurrence in days after imbibition has begun	External appearance of main axis of plant in field
1	--	
2	--	
3	2 (45 hours)	
4	4	Emergence from soil
5	7	Coleoptile and first foliage leaf
6	9	One or two foliage leaves
7	11	Two foliage leaves
8	12	Two or three foliage leaves
9	13	Three foliage leaves
Inflorescence branch primordia	15	Three or four foliage leaves
	17	Four foliage leaves
	21	Five foliage leaves
	27	Six foliage leaves
	33	Seven foliage leaves
	39	Eight foliage leaves
	45	Nine foliage leaves--flag leaf
	53	Emergence of panicle

The main culms of the three varieties observed in this study invariably gave rise to nine foliage leaves. There are rarely more than five expanded leaves visible at any one time during the growing season, and only the last two or three are functional at maturity.

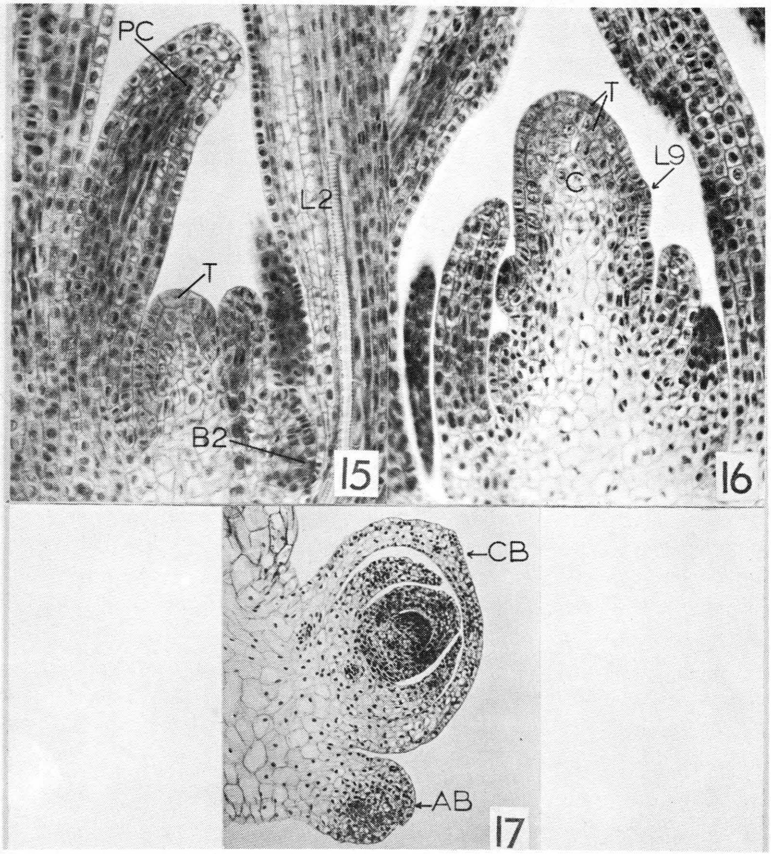


Figure 15. Shoot apex at emergence from the soil. This stage is just prior to the initiation of the fifth leaf. (4 days after planting, X 100)

Figure 16. Shoot apex at initiation of ninth foliage leaf. Note the indication of a two-layered tunica. (13 days after planting, X 100)

Figure 17. Main bud and accessory bud in the axil of the coleoptile. (17 days after planting, x 50)

Procambium	(PC)	Corpus	(C)
Second foliage leaf	(L2)	Tunica	(T)
Third foliage leaf	(L3)	Main coleoptile bud	(CB)
Ninth foliage leaf	(L9)	Accessory coleoptile bud	(AB)

Initiation of axillary buds and development of tillers—Bud initiation is obvious when a visible swelling occurs in the axil of a leaf primordium; however, mitotic activity on the lateral surface of the adjacent unexpanded internode foreshadows the initiation of a bud primordium long before a definite protuberance is evident.

In longitudinal section, cells in the corpus just beneath the protoderm (dermatogen) undergo periclinal divisions which give rise to a region of radially seriated cells, a stratified zone or 'shell zone' (Fig. 18). The bud initials soon become distinct from the larger corpus cells due to their more intense staining and their filar arrangement.

Continued activity in the entire sector leads to an enlargement of the tunica and corpus initials of the bud. At this stage a small protuberance is evident as a consequence of the increase in cell size and number (Fig. 19).

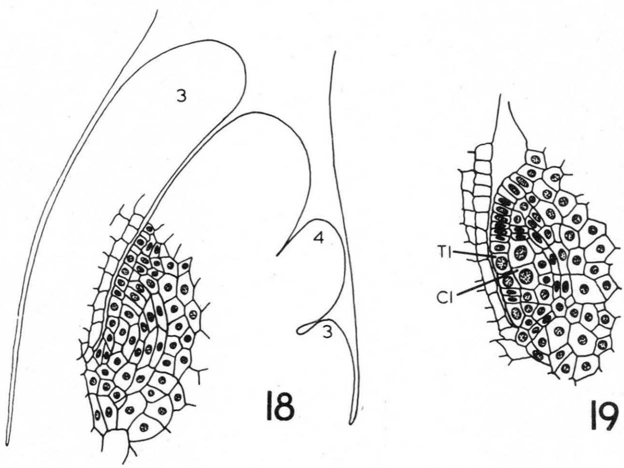


Figure 18. Stratified ("shell") zone which foreshadows the initiation of a bud in the axil of the third foliage leaf. (7 days after planting, X 275)

Figure 19. Bud primordium with tunica and corpus initials. (X 200)
Tunica initials (TI)
Corpus initials (CI)

An axillary meristem with distinguishable tunica and corpus is thus produced. At no time during the course of lateral bud initiation are periclinal divisions to be detected in the tunica.

A stratified zone first becomes evident in the axil of the second leaf primordium from the stem apex. A definite protuberance with tunica and corpus can be observed first in the third or fourth leaf axil from the apex.

Axillary buds on the main axis are initiated acropetally at intervals of 2 to 4 days. The term main axis is used to designate the culm that arises from the plumule. A culm that arises from an axillary bud is designated a tiller. Although the phytomer is considered to be the morphological unit of growth in the shoot, it is more convenient to consider an axillary bud with the leaf which subtends it. Therefore, buds 1 through 5 in Table 2 refer to lateral buds occurring, respectively, in axils of the first five foliage leaves of the main axis.

Four primary axillary buds are invariably initiated, each of which has six or seven leaves (Table 2). The primordium of a bud can occasionally be detected in the fifth leaf axil. During the examination of material for

Table 2. Development of axillary buds[a] as related to time of initiation and subsequent ontogeny

Bud		Days after planting		
On main axis	On tillers	Initiation of bud	Floral transition	Total number of leaves
C (coleoptile)		--	17	6
C^1 (accessory coleoptile bud)		5	--	2
1		$2\frac{1}{2}$	17	7-8
	1			6
	2			5
	3			3
	4			0-1
2		$3\frac{1}{2}$	17	7
	1			3
	2			2
	3			1
	4			0-1
3		5	19	6
	1			3
	2			1
	3			0-1
4		7	19	6
	1			3
	2			1
	3			1
5		11	--	0-2

[a]An axillary bud is designated by the same number as the leaf which subtends it.

this study, there was no external indication of bud initiation in axils of foliage leaves 6 through 9 of the main axis.

Development of primary and higher orders of buds follows the same general pattern as that previously outlined for the main axis. The prophyll of the lateral shoot arises on the adaxial side of the bud primordium and resembles a coleoptile in morphology and development. The prophyll is somewhat flattened on the side facing the main axis and has a longitudinal opening extending down the opposite side. The prophyll has two prominent laterally situated vascular bundles. Succeeeding leaves of the bud arise with two-ranked phyllotaxy at a divergence of 90° to those on the main stem.

By the fifth day after planting a small protuberance is evident on the internode above the base of the coleoptile, just beneath the developing coleoptile bud. This represents the primordium of a second reduced or "accessory" coleoptile bud. Whereas the original coleoptile bud may have a total of six leaves, the accessory bud was observed to develop no further than the two-leaf vegetative stage (Fig. 17).

Under the field conditions of this study, one to three of the axillary buds on the main axis produced panicle-bearing culms. The usual number was two, arising from axillary buds 1 and 2. The main axis enters floral transition by 15 days. By 17 days, buds in the axil of the first two foliage leaves and the larger bud in the axil of the coleoptile had undergone transition. In a count of 132 plants, only two had developed productive fruiting tillers arising from the coleoptile bud. Microscopic examination of all tiller buds at 40 days indicated that all apices eventually produce at least rudimentary inflorescence primordia.

DISCUSSION

The apical meristem of the post dormant embryo and young seedling has a distinct tunica-corpus organization. Divisions in the single-layered tunica are anticlinal except at the point where a new leaf primordium is initiated. Cells of the corpus divide in random planes. During the initiation of the last three or four foliage leaves, the outer cells of the corpus appear to be periclinally stratified. Sharman (1945) has identified four zones in the apex of *Agropyron repens*: dermatogen, hypodermis, subhypodermis, and central core. Hamilton (1948) extended this interpretation to *Avena*. Kleim (1937) interpreted these zones in the *Avena* shoot apex as stratification of the corpus. Although divisions in the subtunica layers are predominantly anticlinal, periclinal divisions are occasionally found prior to floral transition. The doubtful autonomy of such layers and their absence in the early stages suggests a preference for the designation of the apical meristem as a corpus enclosed by a one or two layered tunica. This would be compatible with the occurrence of a two-layered tunica during organogeny as reported by Holt (1953).

The apical meristem of the shoot in *Avena* contains a zone of three to five large corpus cells at the tip. Cells of the tunica adjacent to this region are also larger. Immediately proximal to this zone are linear files of cells which are derivations of the former.

The same pattern of apical initials is established early in the ontogeny of axillary buds. Two or three large corpus initials and two or three large tunica initials are evident by the time a small bud protuberance is initiated. This organization lends evidence in favor of the concept of an apical meristem being composed of a small zone of initials and their derivatives, rather than clear-cut, permanently defined layers and their derivatives.

A general increase in the size of the apical meristem is evident during successive plastochrons of the Avena shoot apex: the increase in volume results from an increase in cell number. Hamilton (1948) reported a slight decrease in cell size of the meristem of Avena during later stages. Occurring with the general increase in size of the apical meristem is a rapid lengthening of the stem tip and an associated shortening in the duration of successive plastochrons.

Sharman (1942b) speculated that, in Agropyron, the marginal meristem of a leaf primordium is concerned with the formation of the bud which will later appear in the axil of the leaf below. This interpretation does not appear applicable in Avena since divisions foreshadowing the initiation of a bud are present before the leaf meristem completely surrounds the stem. Furthermore, the initial periclinal divisions associated with bud formation are relatively deep within the corpus, whereas those associated with the leaf are relatively superficial. (Figs. 7, 8, 9)

The total number of foliage leaves has previously been reported in oats to vary from six to eight (Hamilton, 1948; Holt, 1955). However, in the varieties used in the present studies on Avena, the number of foliage leaves was invariably nine. This was determined by numerous careful dissections throughout the growing season and by examination of serial paraffin sections of the shoot apex at different stages of development. The question of whether leaf number is a constant feature of a variety or whether it is environmentally controlled should be studied further.

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TILE DRAINAGE EXPERIMENTATION ON WEBSTER SOILS: RESULTS OF YEARS 1954-1963[1]

A.S. Rogowski, W.D. Shrader, H.P. Johnson and Don Kirkham[2]

ABSTRACT. In 1953 a drainage experiment was installed on the Clarion-Webster Experimental Farm at Kanawha, Iowa. This experiment on Webster silty clay loam was established to determine the effect of a range of tile spacings on rapidity of drainage, and on crop yields, and to determine if land in alfalfa or in a rotation containing alfalfa is easier to drain than is land in continuous corn. Tile spacings of 100 and 200 feet were studied. During the period 1954 through 1963 there was no difference in average crop yields associated either with tile spacing or with cropping systems.

Differences in rates of drainage are apparently associated with differences in permeability of substrata within the experimental area, rather than with imposed treatment differences.

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INTRODUCTION

Background

In the Clarion-Webster Soil Association area in north-central Iowa, there are about 3.2 million acres of land that have poor natural drainage. Most of these wet lands, which are the Webster or related soils, have been tiled. Present drainage conditions range from good to poor.

While most of the land is tiled, many of the systems are 50 to 70 years old and are in need of repair or replacement, and some areas have never been properly drained. There is, therefore, a continuing need for information concerning drainage in Webster soils.

The need for additional research on drainage has been recognized for years by the farmers of north-central Iowa and by the Agricultural Experiment Station staff.

This interest in drainage problems resulted in the formation of the Clarion-Webster Experimental Association in 1948. In 1952, this association purchased 80 acres of land 1 1/2 miles south of Kanawha to be used by the Iowa Agricultural Experiment Station primarily for research on drainage problems on Webster soils.

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[1] Journal Paper No. J-5196 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project No. 1003. Contribution from the Departments of Agronomy and Agricultural Engineering.

[2] Research Associate Agricultural Engineering and Agronomy; Professor Agronomy; Professor Agricultural Engineering; and Professor Agronomy, respectively.

Objectives

In 1953, an experiment was started to obtain answers to the following questions:

1) What is the effect of a range of tile spacings on the length of time that the land stays wet following rain?
2) What is the effect of different tile spacings on crop yields?
3) What is the effect of different crops on drainage needs? Specifically, there is interest in knowing if land in alfalfa or in a rotation containing alfalfa is easier to drain than is land in continuous corn.

Procedure

To answer the questions listed, the field experiment shown in Figure 1 was installed in 1953. Tile spacings at 100 and 200 feet each at depths of 4 feet were studied. On each tile spacing, 3 management treatments were included: continuous corn, continuous alfalfa and a rotation of corn-corn-oats-meadow. A split-plot design with 4 replications, in which the whole plot is the tile spacing and the split plot the management treatments, was used. The split plot consisted of an area 200 x 70 feet, and the whole plot was 420 x 200 feet and, since large borders were necessary at the ends of the whole plots, the experiment required a relatively large amount of land.

By the use of soil tests and leaf samples as guides, fertilizer rates were adjusted so that fertility was not considered limiting.[3]

Continuous alfalfa was seeded and maintained as a hay crop until the stand became thin on any of the plots, at which time all continuous alfalfa plots were plowed and reseeded. It was necessary to reseed these plots in 1956 and 1963.

The effect of management treatments and of tile spacing differences on drainage were determined by measuring the rate of all of the water table midway between the tile lines and 5 feet from the tile lines. Yield samples were also collected at these same sites.

Description of Experimental Area

As can be seen in Figure 2, all plots in the drainage experiment are located on Webster silty clay loam or on Webster silty clay loam calcareous variant. The 80-acre tract was selected only after an extensive search and was considered to be a highly uniform area of Webster soils. After the field was acquired, a very detailed soil map was prepared, and this map was used in determining the plot locations. The upper 40 inches of the profile are very uniform over the entire experimental area.

When the tile lines were installed, it became evident that the subsoil material below a depth of some 3.5 feet was highly variable. Large areas

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[3] All corn received a uniform starter fertilizer of 5 + 9 + 17. In addition, continuous corn received 120 + 18 + 17, 1st-year corn received 40 + 26 + 25 and 2nd year corn received 80-0-0. Oats received a 20 + 35 + 66 fertilization. The continuous alfalfa was fertilized at a rate of 0 + 35 + 66 biennially.

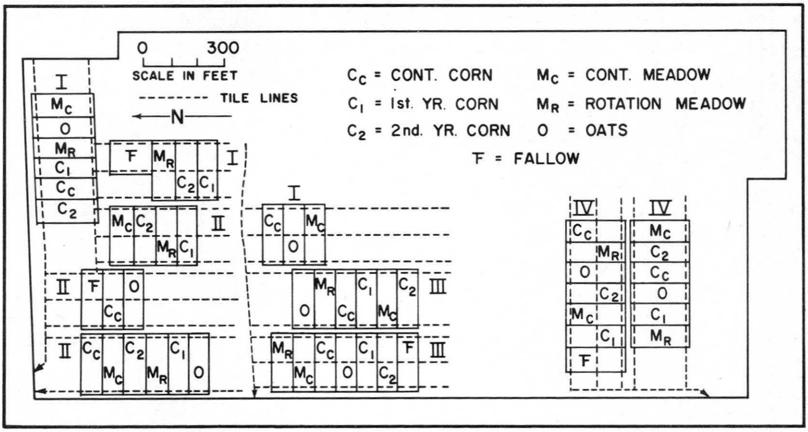

Figure 1. General layout of drainage experiment on the Clarion-Webster Experimental Farm at Kanawha, Iowa showing the location of tile lines and replications; cropping system in 1963 is given for reference.

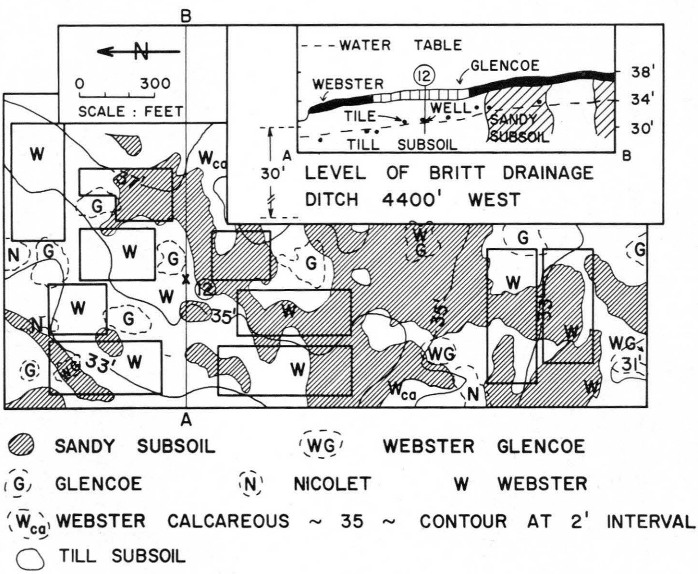

Figure 2. Location of experimental areas of Figure 1 with respect to soil type, subsoil type and contour of the land on the Clarion-Webster Experimental Farm at Kanawha, Iowa; insert gives a cross section, through test well 12, along the line A-B shown in the main part of the Figure.

had loam subsoils, but equally large areas were underlaid by sands and gravels. As a result of further extensive study, the major areas underlain by sand were delineated as shown in Figure 2. The extreme variation is somewhat more obvious in the labeled cross section in Figure 2 (see insert in Figure 2). These sandy substrates were described in detail by White (1953).

The Webster soils are Humic Glei soils that are considered to be formed from glacial till of late Wisconsin age. On the experimental tract, the studies of White (1953) indicate that the parent material is probably lacustrine in the solum overlying outwash material.

The surface 10 to 12 inches is a black (10YR 2/1) silty clay loam with a well-developed fine granular structure. The reaction ranges from slightly acid to calcareous. From a depth of about 12 to 20 inches the soil is a very dark gray (10YR 3/1) silty clay loam with a moderately well-developed fine subangular blocky structure. At a depth of 20 to 24 inches, the soil grades into a gray (10YR 4/1) silty clay loam to loam which becomes somewhat mottled with yellowish-brown at depths below about 30 inches. In places, as already mentioned, this soil continues with little textural change to a depth of several feet. In other places, as shown in Figure 2, the subsoil textures are highly varied.

The hydraulic conductivity (K) of the upper 2 feet has been measured at 8.80 ft/day. Hydraulic conductivity (K) in the till substrate was found to be about 1.04 ft/day in the 2.0 to 3.5 foot layer and 3.76 ft/day in the 3.5 to 5.0 foot layer. Hydraulic conductivities (K) of as much as 10.4 ft/day were found in the sandy subsoils.

The sandy subsoil condition was found by Nielsen (1958) to be in the form of discontinuous pockets. Therefore, even the detail shown in Figure 2 is probably not sufficient to indicate all the variation that actually exists.

RESULTS

Crop Yields

Corn

Yields of continuous corn and of first- and second-year rotation corn at different locations on the 100- and 200-foot tile spacings are given in Table 1 for 1954 through 1963.

On the average, there have been no differences in corn yields due to either rotation or tile spacing. Yields in all systems have averaged the same midway between tile as near the tile. Yields of continuous corn have averaged the same as rotation corn (98.0 as compared to 97.3 bushels per acre), and second-year corn yields have been about the same as first-year yields (95.7 as compared to 97.3 bushels per acre).

The experiment is designed so that every crop is grown every year. Thus, the continuous corn is grown on the same plot each year, and the rotation crop on the same plot once every 4 years. Yield differences may result not only from the treatment differences, tile spacings and rotations, but also from weather (seasonal) differences, and from soil differences.

When the total area of all plots each year is used as in Table 1, yield

Table 1. Yield of corn near tile (NT) and midway between tile (MT) for continuous corn, first-year corn and second-year corn, 1954 to 1963, on the drainage experiment at the Clarion-Webster Experiment Farm at Kanawha, Iowa

Kind of corn	Tile Spacing	Plot Location	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	Average
			Yield of corn in bushels per acre										
Continuous corn	100'	NT[1]	100.9	37.4	77.6	106.1	94.8	107.5	89.2	117.8	109.1	141.4	98.2
		MT[2]	88.0	42.2	76.3	104.9	91.7	105.6	94.2	129.0	101.5	134.3	96.8
		Spacing Average	94.5	39.8	77.0	105.5	93.3	106.6	91.7	123.4	105.3	137.9	97.5
	200'	NT	89.4	52.1	86.6	102.2	99.8	111.3	89.0	122.4	104.6	134.2	99.2
		MT	88.9	50.0	82.2	104.6	92.9	109.0	95.3	127.9	99.3	127.9	97.8
		Spacing Average	89.2	51.1	84.4	103.4	96.4	110.2	92.2	125.2	102.0	131.0	98.5
		C_c Average	91.9	45.5	80.7	104.5	94.9	108.4	92.0	124.3	103.7	134.5	98.0
1st year corn	100'	NT	95.8	60.7	65.0	100.4	89.1	113.7	83.5	117.1	111.1	146.7	98.3
		MT	94.3	62.8	70.7	94.0	86.1	115.1	81.9	119.0	109.0	147.3	98.0
		Spacing Average	95.1	61.8	76.9	97.2	87.6	114.4	83.2	118.1	110.1	147.0	98.2
	200'	NT	94.7	60.1	76.0	97.6	95.5	99.3	79.6	106.9	114.1	145.7	97.0
		MT	88.8	58.3	80.1	92.8	89.2	100.5	70.7	124.0	109.1	143.0	95.7
		Spacing Average	91.8	59.2	78.1	95.2	92.4	99.9	75.2	115.5	111.6	144.2	96.3
		C_1 Average	93.5	60.5	73.0	96.2	90.0	107.2	79.2	116.8	110.9	145.6	97.3
2nd year corn	100'	NT	98.3	41.5	81.8	103.2	83.8	104.8	86.8	114.1	100.2	143.1	95.8
		MT	91.4	50.3	89.3	100.4	82.1	101.4	89.2	120.2	102.7	138.5	96.6
		Spacing Average	94.9	45.9	85.6	101.8	83.0	103.1	88.0	117.2	101.5	140.8	96.2
	200'	NT	96.4	42.4	82.1	101.4	80.6	106.8	85.6	102.4	106.3	140.9	94.5
		MT	87.2	48.7	90.1	99.3	78.2	107.9	81.7	119.0	103.4	139.1	95.5
		Spacing Average	92.0	45.8	86.1	100.4	79.4	107.4	83.7	110.7	104.9	140.6	95.1
		C_2 Average	93.5	45.8	85.9	101.1	81.2	105.3	85.9	114.0	103.2	140.7	95.7

[1] NT means: samples were taken 5 feet from the tile.

[2] MT means: samples were taken midway between tiles.

differences due to treatment and to soil cannot be separated. For this reason, a more precise measure of treatment effects is possible when only yields from the same plots are compared because weather and soil factors are then constant.

The results of this type of comparison are shown in Figure 3 in which the average effects of cropping systems within a given year are compared. In this analysis, it was found that yields in the different systems showed significant differences. Yield differences in different systems were slight and do not appear of much value in predicting yields on other fields or in other seasons. Continuous corn outyielded rotation corn 4 out of the 10 years. The four years, when continuous corn yields were higher than rotation corn yields, were years with below-average rainfall; however, one year, when rotation yields were highest, was also a dry year.

When the same type of comparison was used on tile spacing, there was a significant effect at the 5-percent confidence level, or better, in 4 out of the 10 years, and, at the 1-percent confidence level, in three of these years. Yield differences, however, were too small to be of much practical significance.

Corn yields were lower on the 200-foot tile spacing as compared with the 100-foot spacing in 1954, 1958, 1960 and 1961. For these years, yields averaged 97.5 bushels per acre on the land tiled at 200 feet. Since one of the years had above-normal rainfall, while the other three were below normal, and because yields on either tile spacing were quite high, it does not appear that drainage limited yields substantially on any of the plots during the study.

Further detail of effect on corn yield of tile spacing and distance from tile lines is given in Figure 4. Distance from the tile had a significant effect on yield in 4 out of 10 years studied. In 1954, 1958 and 1962, yields were lower midway between tile lines, but in 1961, yields were higher midway between the tile lines as compared with locations near the tile lines. For two of those years (1954, 1961) spacing had a significant effect. But whereas yields were significantly higher on 100-foot spacing (see Figure 4) in 1954, they were significantly lower on the same spacing in 1962.

Oats

A summary of oat yields is given in Table 2. Neither tile spacing nor distance from the tile had a significant effect on oat yields. Yields varied from 64 bushels per acre in 1963, a relatively wet year, to 113 bushels per acre in 1958, a relatively dry year.

However, since intermediate yields were produced in seasons with both higher and lower rainfall, drainage conditions do not appear to have limited oat yields during the period of this study.

Hay

Yields of continuous and of rotation meadows are summarized in Table 3.

The highest yields, about 4.5 tons per acre, were obtained in 1962, which was also the year with the highest rainfall. As is shown in Table 3, the yields of continuous hay for the period of study averaged higher on the

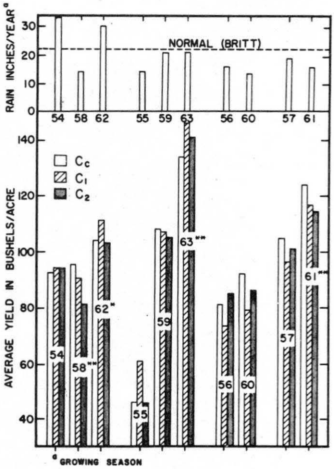

Figure 3. Comparison of yields (1954-1963) of continuous corn (C_c), first year corn (C_1) and second year corn (C_2) obtained on the same plots of the drainage experiment at the Clarion-Webster Experimental Farm at Kanawha. Levels of significance (** = 1% level, * = 5% level) for 4 out of 10 years when significant differences between cropping systems were observed are indicated.

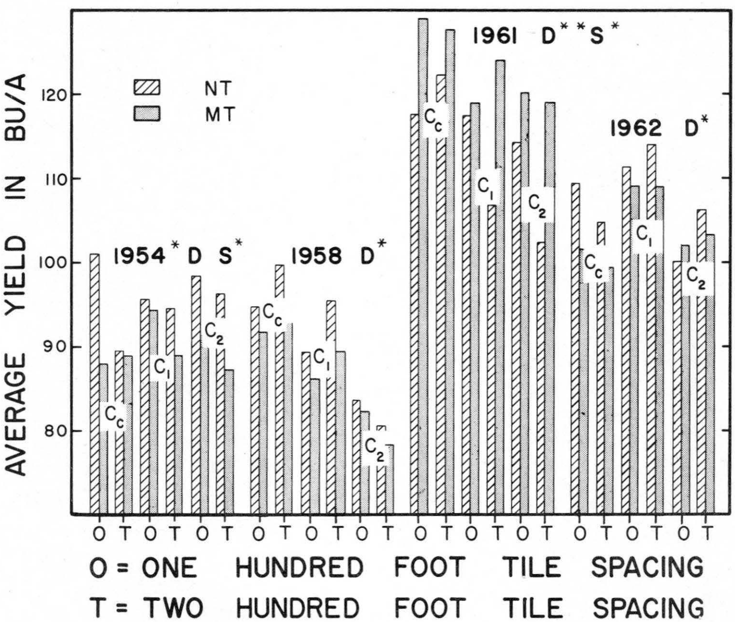

Figure 4. Effect of tile spacing (S) (0 = 100' spacing; T = 200' spacing) and distance (D) from the tile (NT = near tile; MT = midway between tiles) on yield of continuous corn (C_c), first-year corn (C_1) and second-year corn (C_2), for four out of ten years, when distance, spacing or both distance and spacing were significant (** = significant at 1% level, * = significant at 5% level), at the Clarion-Webster Farm at Kanawha, Iowa.

Table 2. Yield of oats 1955-1963, [1] near tile (NT), and midway between tile (MT), on the drainage experiment at the Clarion-Webster Experimental Farm at Kanawha, Iowa

Tile Spacing	Plot Location	1955	1956	1957	1958	1959	1960	1961	1962	1963	Average
		Average yield in bushels per acre									
100'	NT[2]	88.0	79.7	75.1	114.2	83.2	88.9	79.4	86.5	67.0	84.7
	MT[3]	78.0	63.0	66.5	115.1	96.1	97.0	79.6	89.0	61.4	82.9
Spacing Average		83.0	71.4	70.8	114.7	89.7	93.0	79.5	87.8	64.2	83.8
200'	NT	77.3	77.0	72.0	108.3	88.9	102.8	84.5	81.6	63.4	84.0
	MT	78.9	79.6	74.0	116.3	97.5	105.2	75.8	99.6	64.4	87.9
Spacing Average		78.1	78.3	73.0	112.3	93.2	104.0	80.2	90.6	63.9	86.0
Oats Average		80.6	74.8	71.9	113.5	91.4	98.5	79.8	89.2	64.1	84.9

[1]In 1954 samples were taken from plots disregarding the location of title

[2]NT means: samples were taken 5' from the tile

[3]MT means: samples were taken midway between the tile

Table 3. Yield of hay 1957-1962, [1] near tile (NT), and midway between tile (MT), for rotation meadow and continuous meadow on the drainage experiment at the Clarion-Webster Experimental Farm at Kanawha, Iowa

Kind of meadow	Tile Spacing	Plot Location	1957	1958	1959	1960	1961	1962	Average
			Yield of hay in tons per acre						
RM[2]	100'	NT[4]	3.34	1.83	3.57	4.27	3.38	4.42	3.47
		MT[5]	3.30	1.89	3.43	3.58	3.20	4.55	3.32
	Spacing Average		3.32	1.86	3.50	3.93	3.29	4.49	3.40
	200'	NT	3.67	2.13	3.37	3.35	3.82	4.53	3.48
		MT	3.69	2.13	3.26	2.96	3.57	4.48	3.35
	Spacing Average		3.68	2.13	3.32	3.16	3.70	4.51	3.42
	RM Average		3.50	2.00	3.41	3.54	3.49	4.50	3.41
CM[3]	100'	NT	3.47	2.87	3.09	3.55	3.22	4.10	3.38
		MT	3.63	2.88	3.03	2.88	2.49	3.76	3.11
	Spacing Average		3.55	2.88	3.06	3.22	2.86	3.93	3.25
	200'	NT	3.78	3.12	3.65	3.53	3.62	4.24	3.66
		MT	3.46	3.10	3.19	3.10	3.14	3.94	3.32
	Spacing Average		3.62	3.11	3.42	3.32	3.38	4.09	3.49
	CM Average		3.59	2.99	3.24	3.27	3.12	4.01	3.37

[1]In 1955 only first cutting was reported, second cutting was not taken because of poor stand. In 1956 and 1963, cont. meadow was reseeded and no data are available.

[2]RM means: rotation meadow.

[3]CM means: continuous meadow.

[4]NT means: samples were taken 5' from the tile lines.

[5]MT means: samples were taken midway between the tile lines.

200-foot as compared with the 100-foot tile spacing. It therefore appears that drainage, either at the 100- or 200-foot spacing, did not limit hay yields. However, as is also shown in Table 3, hay yields averaged higher near the tile as compared with hay yields midway between tile lines.

Hydrologic Results

Rainfall

In Table 4, average monthly precipitation from 1954 through 1963 is given. The data for the growing season months (April through September) were obtained with a recording rain gauge at the Clarion-Webster Experimental Farm. The data for other months as well as the long-term normal average growing season precipitation are for Britt, Iowa, which is 11 miles north of the Clarion-Webster Experimental Farm. During the past decade, as is shown in Table 4, growing season rainfall was above average only in 1954 and 1962 at the Clarion Webster Experimental Farm. These two occasions also correspond to the two times that the level of the water table rose to the surface of the ground.

Water table drawdown

According to Grover (1954), the water tables in 1954 were not high enough to make readings except for a short period in June. The storm at this time was quite intense (10 inches in 24 hours), and much water accumulated in low areas. The water table level was quite erratic and soon fell below reading depth. No conclusions could be drawn because the readings taken did not show any consistent differences.

In 1962, the water tables were high enough to make readings only for a short period at the end of August and the beginning of September. At that time, a heavy rainfall (6 inches in 48 hours) brought the water table to the surface of the ground. After 3 days (Figure 5), the water table level fell below reading depth. The results are based on the three sets of observations started 8 hours after the water table was at the ground surface and were taken at 24-hour intervals thereafter. Details of water table fall for this storm of August 1962 are reported since it is the only storm aside from that mentioned by Grover, during which a high water table occurred.

In the tests of August 1962, the drawdown results for each plot are based on the readings obtained from 4 piezometer pipes per 200 x 70 foot plot (see Figure 1). Two piezometer pipes are located 5 feet from the tile line (NT), and two are located midway between tile line (MT). All results obtained from the plots are averaged for each spacing (100 or 200 feet) and each location (NT or MT). All results obtained from plots with the same crop are also averaged for each spacing, location and crop (continuous corn, first-year corn, second-year corn). Finally a possible influence of the type of subsoil (sand or till) is investigated on both spacings and locations.

Comparison of tile spacings for the storm of August 1962

In Figure 5, the average drawdown for both 100- and 200-foot tile spacing is presented. After an initial 8 hours of drawdown on 100-foot spacing midway between the tile lines, the water table fell 16 inches

Table 4. Average monthly precipitation[1/] in inches, for 1954-1963, for the Clarion-Webster Experimental Farm at Kanawha, Iowa

	Year										
Month	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	Normal
	Inches of rain										
April	5.33	2.06	1.05	0.96	2.40	1.30	1.75	1.94	2.13	3.29	2.34
May	3.35	1.37	4.26	5.10	2.40	4.60	4.45	2.48	5.09	3.39	3.62
June	13.09	1.53	1.86	4.50	3.50	3.70	1.81	2.08	4.67	3.10	5.44
July	1.74	3.52	4.79	3.14	4.20	0.80	0.50	2.48	6.58	6.45	3.49
August	5.26	2.54	1.28	3.40	0.80	5.00	2.83	3.00	10.14	2.69	3.93
September	2.49	2.96	2.09	1.67	1.00	4.40	2.56	4.29	1.63	1.60	3.41
Growing Season Total	31.26	13.98	15.33	18.77	14.30	19.80	13.90	16.27	30.24	20.52	22.23
January	0.76	0.77	0.98	0.59	0.71	0.40	0.32	0.30	0.25	0.87	1.05
February	1.29	1.58	0.40	0.38	0.15	1.99	0.89	2.30	2.32	0.96	1.00
March	2.05	1.69	3.69	1.73	0.59	2.62	1.09	3.91	1.48	1.14	2.07
October	3.52	1.74	1.43	1.55	0.11	1.81	0.56	3.86	1.17	0.71	1.78
November	0.42	0.74	2.45	3.70	0.74	1.91	0.79	1.47	0.13	1.09	1.63
December	0.70	1.21	0.54	1.14	0.40	1.55	1.46	1.86	0.19	0.51	1.09

1/ Precipitation values for the non-growing season months and for all normal values are from records of Britt, Iowa. Precipitation values for the growing season months were obtained at the farm.

below the ground surface as compared with the 8 inches on the 200-foot spacing. During this time, the tile lines were running under pressure.

On the following day, the water table on 100-foot spacing fell only 4 more inches on the average from what it was 24 hours before, but during the same time, the fall on a 200-foot spacing amounted to 8 inches. Therefore, on the second day, after 32 hours of drawdown, the level of the water table on 100-foot spacing was 20 inches below the fround surface as compared with 16 inches below the ground surface for a 200-foot spacing.

During both the second and the third day, there was no back pressure in the tile lines. On the third day, the water table midway between the tile lines fell another 6 inches on both spacings. Thus, after 56 hours of drawdown, the water table was 26 inches below the surface of the ground on a 100-foot spacing and 22 inches below the surface of the ground on the 200-foot spacing. The readings of the water table on the fourth day were inconsistent and variable to the extent that no average depth of the water table could be established.

Rate of water table drawdown: tile spacing

In Figure 6, the rate of water table drawdown on 100- and 200-foot tile spacing near the tile lines (NT) and midway between the tile lines (MT) is illustrated. During the initial 8 hours, the rate of fall of the water table was greater on a 100-foot spacing than on a 200-foot spacing, both near (NT) and midway (MT) between the tile lines. During the following 2 days (periods of 24 hours each), Figure 6 shows that the rate of fall of the water table was essentially the same on 100-foot spacing as it was on a 200-foot spacing. This suggests deep seepage (translocation of water below the tile) into interlocking subsoil sand lenses having outlets of lower elevation.

Rate of water table drawdown: crop[4]

The rate of water table drawdown midway between the tile lines on 100- and 200-foot tile spacings on continuous corn, first-year corn and second-year corn is illustrated in Figure 7. Midway between the tile lines, both continuous and second-year corn exhibited the same rate of drawdown for the first 32 hours on both spacings. Although the rate of drawdown on the second-year corn for the last 24 hours remained essentially the same for both spacings, the rate of drawdown on 100-foot spacing of continuous corn was greater than on 200-foot spacing. This suggests that, although during the first 32 hours, deep seepage could have been influencing the rate of fall of the water table, the effect due to tile spacing, at least on continuous corn, was not obvious until the third day (32 to 56 hours).

In contrast to continuous corn and second-year corn (both of which exhibited the similar rates of drawdown), the rate of drawdown on first-year corn (corn following meadow) was less. In particular, on the second

[4] The drawdown data was obtained only on corn plots. Just prior to the occurrence of the water table, piezometer pipes were withdrawn from all plots in preparation for fall work. Only the piezometer pipes on corn could be replaced in time to obtain the readings.

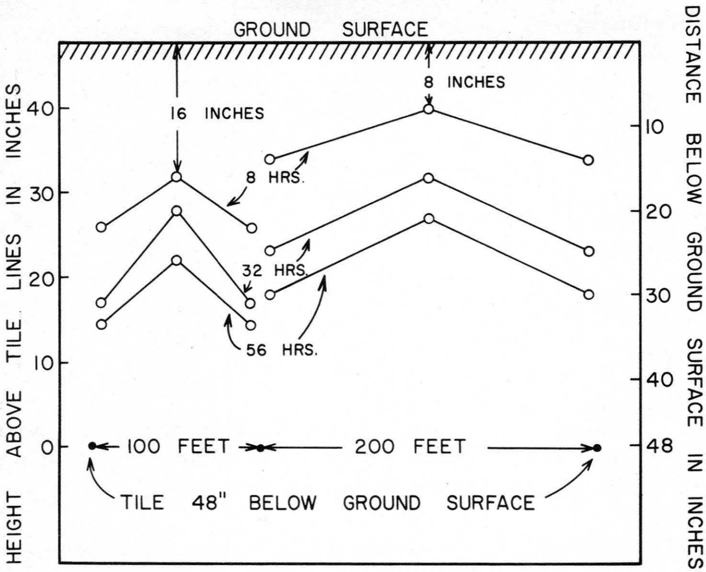

Figure 5. Average water table drawdown on 100-foot and 200-foot tile spacing for a 56-hour period in August, 1962 at the Clarion-Webster Experimental Farm at Kanawha, Iowa.

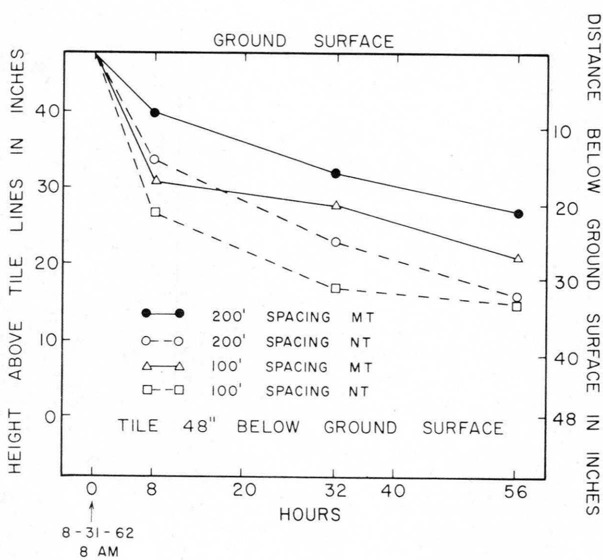

Figure 6. Effect of 100-foot and 200-foot tile spacing on the rate of water-table drawdown for a period of 56 hours in August 1962 near the tile (NT) and midway between tile lines (MT) at the Clarion-Webster Experimental Farm at Kanawha, Iowa.

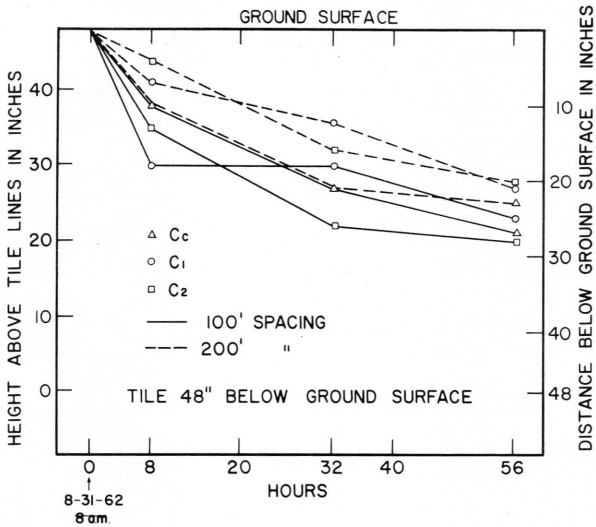

Figure 7. Effect of continuous corn (C_C) first-year corn (C_1) and second year corn (C_2) on the rate of water-table drawdown midway between the tile lines on 100-foot and 200-foot tile spacing for a period of 56 hours in August 1962 at the Clarion-Webster Experimental Farm at Kanawha, Iowa.

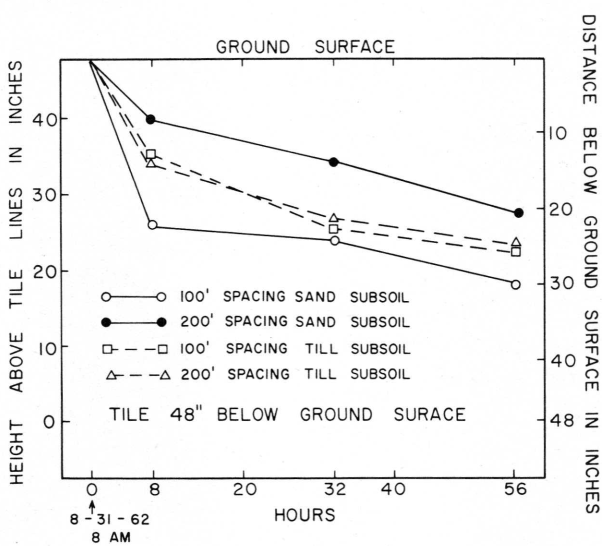

Figure 8. Effect of till and sandy subsoil on the rate of water-table drawdown midway between the tile lines on 100-foot and 200-foot tile spacing for a period of 56 hours in August 1962 at the Clarion-Webster Experimental Farm at Kanawha, Iowa.

day (8 to 32 hours), as can be seen from Figure 7, the rate of drawdown on the first-year corn was almost 0. On the third day (32 to 56 hours), the rate of drawdown increased. The rate of drawdown remained the same on both tile spacings and similar to those observed for continuous and second-year corn, again suggesting deep seepage.

Rate of water table drawdown: type of subsoil

The rates of drawdown on one 100- and 200-foot spacing, midway between the tile lines for the areas underlain by sandy and till subsoil, are given in Figure 8. During the initial 8 hours, the 100-foot spacing underlain by sandy subsoil exhibited the fastest rate of drawdown. In the following 24-hour period (8 to 32 hours), both the 100- and 200-foot spacings underlain by till showed the fastest rate of drawdown, while the 100-foot spacing underlain by sand had a slowest rate of drawdown. In the last 24 hours (32 to 56 hours), both spacings underlain by sandy subsoil exhibited the same rate of drawdown, which was slightly greater than the rate of drawdown observed on two spacings underlain by till subsoil. It was also observed that both spacings of the till and sand subsoil drained at the same rate close to the tile lines.

DISCUSSION OF RESULTS

From the results reported in Figure 5, the indications are that, in the first 8 hours following the occurrence of the water table on the surface of the ground as a result of intense rain, the drawdown on 100-foot spacing was twice the drawdown on 200-foot spacing. After the initial drawdown, there appeared to have been few differences between the spacings. The difference of 7 inches on the 100-foot spacing between the height of the water table midway between the tiles and near the tiles (5 feet from the tile) and a corresponding difference of 11 inches on the 200-foot spacing, 52 hours after the water table was at the surface of the ground, suggests that deep seepage rather than the drawdown resulting from tiling is the primary water-table-level controlling mechanism at the Clarion-Webster Farm.

As indicated in Figure 6, the rate of fall of the water table was the same, except for the difference in the initial 8 hours of drawdown, on both spacings close to as compared with midway between the tile lines. It is also shown in Figure 7 that the rate of drawdown on continuous corn and second-year corn was the same on both spacings for the first 32 hours. After that time, however, the rate of drawdown on 200-foot spacing of continuous corn was less than that on the 100-foot spacing. Since the tiles were running without back pressure during the last 24 hours (32 to 56 hours), the difference in the rate of drawdown between the spacings during the last 24 hours could reflect the difference due to tile spacing.

From a study of Figure 7, it can be seen that the rate of drawdown on first-year corn was different from that on the continuous and second-year corn. In particular, on the 100-foot spacing of the first-year corn, the curve in Figure 7 for the 8- to 32-hour period is practically flat. In Figure 1 and Figure 2, it is indicated that three ouf of four first-year corn plots are underlain by the sandy subsoil, and in Figure 8 we observe that the curve for the drawdown on the 100-foot spacing of the sandy subsoil closely corresponds to that for the first-year corn. It would appear, therefore, that the difference observed in the rate of drawdown on the first-year corn is due to the underlying sandy subsoil rather than to the effect of crop.

A study of the data presented in Figure 8 indicates that, during the initial 8 hours, the rate of drawdown midway between the tile lines was greatest on the 100-foot spacing underlain by sandy subsoil. As is also shown in Figure 8, the rate of drawdown on till subsoil during the second day (8 to 32 hours) was greater than the corresponding rate of drawdown on the sandy subsoil. This perhaps results from the presence of a very slowly permeable layer at the depth of 24 to 41 inches in the till subsoil areas which have been shown to have a permeability expressed by K_1 = 1.03 ft/day as compared with the permeability of K_2 = 8.80 ft/day in the surface layer above it. When the ratio of permeabilities K_2/K_1 is five or greater, very little water will flow through the subsoil. Most of the water must flow laterally through the surface soil to reach the more permeable material (Luthin, 1950). It therefore appears probable that the flatness of the 100-foot spacing on sandy subsoil during the second day (8 to 32 hours) was due to the lateral translocation of water from the areas underlain by the till subsoil to the areas where the water table was lowest, such as on the 100-foot spacing on sandy subsoil.

In Figure 8, it is evident that the level of the water table on the 200-foot spacing on sandy subsoil was higher after 32 to 56 hours of drawdown than was the level of the water table of 100-foot spacing on sandy subsoil as well as higher than both spacings on till subsoil. As shown in Figure 1 and 2, five out of seven plots of 200-foot spacing on sandy subsoil are located in such a way that the sandy subsoil areas terminate a little distance beyond the area where midway-between-tile-measurements were taken. It therefore appears probable that the higher level of the water table on these plots resulted from translocation of water laterally through the surface layer from areas underlain by till subsoil located at higher elevations.

CONCLUSIONS

On the basis of results presented, it is concluded that:

1) After the initial 8 hours of drawdown, the average fall of water table on the 100-foot spacing was twice the average fall on 200-foot spacing (16 inches as compared with 8 inches). It also appears that, 32 hours after the water table was at the surface of the ground, there was essentially no difference between the height of water table on either spacing (ca. 18 inches below the ground surface). Also, the height of the water table was not appreciably affected by distance from the tile lines on either the 100-foot or 200-foot spacings. This suggests that the deep seepage is influential in controlling the water table level at the Clarion-Webster Experimental Farm.

2) It does not appear that drainage substantially limited yields on any of the plots during the study. However, for 4 out of 10 years, corn yields were significantly higher on the 100-foot tile spacing than on the 200-foot tile spacing. The difference, 97.5 as compared with 95.3 bushels per

acre was so slight as to be of little practical importance. Furthermore, for 4 out of 10 years, the location with respect to the tile was significant. For 3 out of 4 of these years, the yields were significantly lower midway between the tile lines.

3) It did not appear that the land in rotation containing alfalfa was easier to drain than land in continuous corn. The slower rate of drainage on the first-year corn plots can be traced to the nature of underlying subsoil.

4) The drawdown on the Clarion-Webster Experimental Farm appears primarily the result of two mechanisms. The first is deep seepage (translocation of water below the tiles); the second is the translocation of water laterally through the surface layer on the soil underlain by till.

5) The results presented and the conclusions drawn should be considered in the light of evidence that the rainfall during the preceding 10 years was below normal for 8 out of 10 years. The water table rose to the surface of the ground only twice during the past decade, and both times, this rise was caused by intense heavy rainfall.

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GROWTH OF EASTERN COTTONWOOD IN RELATION TO COAL-SPOIL CHARACTERISTICS[1]

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ABSTRACT. A study was made of growth of eastern cottonwood in relation to selected characteristics of Iowa coal-spoil materials. The objectives were: 1) Determine if the past and current growth of this species is related to the chemical characteristics of the spoils. 2) Identify those factors most closely related to cottonwood growth. 3) Provide this information to permit formulation of hypotheses for future controlled experiments. Total tree height was related to the percentage of soil-size material in the spoils and to some spoil nutrients. Variation in tree height was best accounted for by soluble salt concentration, exchangeable and soluble Ca and percentage of soil-size material. Tree height increment in 1961 was related to the mineral composition of the leaves. Variables related to the 1961 increment were foliar N, P, K and Mg. Height increment and foliar Mg were inversely related. Foliar N and initial tree height accounted for 42 per cent of the variation in height increment. The foliar N-height increment relationship suggests that nitrogen and phosphorus deficiencies are limiting tree growth at least on some coal-spoil materials.

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Successful establishment and good growth of desirable vegetation on land stripped for coal is not easily attained. Few desirable tree species have grown well on the extreme sites usually associated with coal-spoil materials (1, 4, 6, 7, 8 and 11). Additional information is needed on the relationship of tree survival and growth to coal-spoil characteristics before successful establishment and good growth of many tree species will be realized. In an earlier study, Lorio and Gatherum (9) related survival and growth of several planted tree species, including eastern cottonwood

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(Populus deltoides Bartr.), to selected properties of spoil materials. Moreover, cottonwood has survived satisfactorily and has made poor to good growth on a wide variety of coal-spoil materials in Iowa (4, 8, 9); consequently, a more detailed study was established of the growth and development of young cottonwood trees in relation to selected chemical and physical characteristics of the coal-spoil materials. The results of this study are presented in this paper.

The objectives of this study were to determine the past and current growth of eastern cottonwood on a variety of coal-spoil materials, and thus: 1) determine if growth of this species is related to the chemical characteristics of the spoils, 2) identify those factors most closely related to cottonwood growth, and 2) provide this information to permit formulation of hypotheses for future controlled experiments designed to identify cause and effect relationships between chemical characteristics of the spoil materials and the growth of cottonwood.

METHODS

The study areas, located in Marion, Mahaska and Wapello Counties in southeastern Iowa, are within 10 miles of the Des Moines River and represent the general classes of coal-spoil material described by Einspahr (4).

Location	Spoil Type
Pella	- calcareous glacial till, pH 7.5 to 7.9.
Pershing	- sandy buff shale, pH 6.4.
Otley	- brown shale, pH 4.0 to 4.5.
Oskaloosa	- black calcareous shale, pH 7.2 to 7.7.
Kirkville	- glacial till and gray shale, pH 4.0 to 6.0.

However, the surface material within each area varies greatly; therefore, the general description of areas probably does not adequately describe conditions on each plot.

Twenty single-tree plots were established in each of the five areas to insure a range of tree vigor from poor to good. Tree and surface spoil material data were obtained from each of the 100 single-tree plots for simple and multiple correlation and regression analyses. Variables studied and the range of values found for each are shown in Table 1.

Measurements and Analyses

Total height of each tree was measured in 1961 before leader growth had begun in the spring and at the termination of growth in the fall. Height increment for the 1961 growing season was taken as the difference between the spring and fall measurements. Age of each tree was determined by ring counts of increment cores taken 1 foot above the base. Counts were made in the laboratory after the cores were stained with phloroglucinol, as described by Patterson (10).

Leaf samples were collected between August 26 and August 30, 1961

Table 1--Variables studied and the range of values found for each.

Variables	Range of values		
Y_1 - total height (feet)	6.7	to	40.5
Y_2 - height increment (feet)	0.0	to	10.3
X_1 - acidity (pH)	2.8	to	8.1
X_2 - exchangeable aluminum (me. per 100g.)	0.00	to	7.21
X_3 - exchangeable hydrogen (me. per 100g.)	0.00	to	2.22
X_4 - exchangeable and soluble calcium (me. per 100g.)	0.99	to	71.45
X_5 - exchangeable and soluble magnesium (me. per 100g.)	0.00	to	7.65
X_6 - available phosphorus (pounds per acre)	0.5	to	33.5
X_7 - available potassium (pounds per acre)	13	to	>360
X_8 - sum of calcium, magnesium and potassium (me. per 100g.)	1.01	to	79.56
X_9 - soluble salt concentration (parts per million)	<50	to	4370
X_{10} - nitrifiable nitrogen (pounds per acre)	4	to	78
X_{11} - soil air permeability (mm. per second)	0.05	to	1.85
X_{12} - field capacity (per cent by weight)	11.5	to	46.9
X_{13} - soil-size material (per cent by weight)	75.2	to	100.0
X_{14} - tree age (years)	9	to	19
X_{15} - foliar nitrogen (per cent by weight)	1.39	to	4.00
X_{16} - foliar phosphorus (per cent by weight)	0.10	to	0.34
X_{17} - foliar potassium (per cent by weight)	0.46	to	2.58
X_{18} - foliar calcium (per cent by weight)	0.59	to	2.49
X_{19} - foliar magnesium (per cent by weight)	0.12	to	1.67
X_{20} - initial tree height (feet)	5.3	to	36.3

for laboratory analyses of mineral composition. Collection procedure followed that described by Brendemuehl (2).

Foliar nitrogen, phosphorus and potassium were determined in the laboratory of Dr. John Hanway, Department of Agronomy, Iowa State University. A 0.50-gram sample of the dried, ground leaves was digested in H_2SO_4 plus Cu on a hot plate for 24 hours. The digest was diluted with NH_3-free water, and nitrogen was determined by steam distillation of NH_3 from an aliquot made alkaline with NaOH. The NH_3 was trapped in boric acid and subsequently titrated. Phosphorus was determined colorimetrically by a modified vanadomolybdate method. Potassium was determined with a flame photometer with lithium as an internal standard.

Calcium and magnesium were determined in digests of the dry leaf material prepared as described by Jackson (5), except that 2$\underline{N}$ HCL was used to dissolve the salts, followed by filtering for the removal of silica. The milliequivalents of calcium and magnesium were titrated in 10-ml aliquots of a final solution after removal of phosphate and heavy metal interference with zirconyl chloride precipitation and filtration, as described by Derderian (3). Calcium was titrated with approximately 0.01$\underline{N}$ standard ethylenediaminetetraacetic acid (EDTA) at pH 13, with calcon as the indicator. The sum of calcium plus magnesium was titrated with the same EDTA solution at pH 10, with Eriochrome Black T as the indicator, and magnesium was determined by difference.

Composite samples were taken of the coal-spoil materials to a depth of 6 inches under the crown of each tree in the spring of 1961. The samples were analyzed for percentage of soil-size material ($<$2mm), pH, exchangeable and soluble calcium and magnesium, exchangeable aluminum, exchangeable hydrogen, soluble salt concentration, nitrifiable nitrogen, available phosphorus and available potassium. All analyses, except those for nitrifiable nitrogen and available potassium, were made with air-dry samples which had been crushed and passed through a 2-mm sieve. Determinations of nitrifiable nitrogen and available potassium were made at the field moisture content, and the results corrected to a standard 25% moisture content. Methods of analyses have been described by Lorio and Gatherum (9).

Field capacity and air permeability at field capacity were determined <u>in situ</u>. Ten-inch-diameter furnace pipe was driven 3 inches into the ground in the vicinity of each tree. A 6-inch water equivalent of rainfall was added, and the top was covered with plastic to prevent evaporation. After 2 or 3 days, the plastic was removed, and the air permeability was measured with a sphygmomanometer, as described by Wilde and Steinbrenner (12). Field capacity was determined gravimetrically.

RESULTS AND DISCUSSION

Correlation of Tree Height and Growth with Coal-Spoil Characteristics

Chemical characteristics correlated positively with tree height were acidity, exchangeable and soluble calcium, available potassium, nitrifiable nitrogen, and the sum of calcium, magnesium and potassium (Table 2). Exchangeable aluminum and exchangeable hydrogen were correlated negatively with tree height. No relationships were indicated with field

Table 2--Correlation coefficients (r) and coefficients of determination (r^2, in %) for total height (Y) and significant coal-spoil variables.[1]

Variable	r	r^2
X_1 - acidity (pH)	0.48**	23.04
X_2 - exchangeable aluminum (me. per 100 g.)	-0.37**	13.69
X_3 - exchangeable hydrogen (me. per 100 g.)	-0.33*	10.89
X_4 - exchangeable and soluble calcium (me. per 100 g.)	0.33*	10.89
X_7 - available potassium (pounds per acre)	0.35*	12.25
X_8 - sum of calcium, magnesium and potassium (me. per 100 g.)	0.30*	9.00
X_{10} - nitrifiable nitrogen (pounds per acre)	0.41**	16.81
X_{13} - soil-size material (per cent by weight)	0.45**	20.25
X_{14} - tree age (years)	0.61**	37.21

[1]n = 100; df = 98; **significant at 1% level; *significant at 5% level.

capacity or air permeability, but percentage of soil-size material was correlated positively with tree height.

The correlations indicate that higher amounts of fine material were related to higher fertility and better tree growth. The air permeability and field capacity of the surface material, in the range encountered in this study, are not important indicators of the quality of the spoil material for tree growth. Correlation coefficients were generally lower than found in an earlier study of yield on replicated plots, where all trees were the same age, planted on similar slope and aspect, and yield represented a weighted average of a number of trees (9).

Height increment for 1961 was correlated positively with initial tree height and foliar nitrogen, phosphorus and potassium (Table 3); a somewhat unusual and interesting result, however, was the negative correlation of height increment with foliar magnesium. In addition, foliar magnesium was inversely related to foliar nitrogen, phosphorus and potassium.

Height increment was most closely related to foliar nitrogen and then to foliar phosphorus. The correlation of foliar nitrogen with nitrifiable nitrogen of the spoil material (Figure 1) and the close relation between foliar nitrogen and foliar phosphorus (Figure 2) suggest that nitrogen and phosphorus may be important factors affecting tree growth on these spoil materials. Similarly, Brendemuehl (2), in a study of cottonwood growth on bottomland soils in Iowa, found that foliar nitrogen and soil nitrifiable

Table 3--Correlation coefficients (r) and coefficients of determination (r^2, in %) for height increment (Y), initial height and foliar nutrients.[1]

	X_{15} Foliar N	X_{16} Foliar P	X_{17} Foliar K	X_{18} Foliar Ca	X_{19} Foliar Mg	X_{20} Initial height
			r			
X_{15} Foliar N	-----	0.69**	0.26*	-0.06	- 0.28*	0.36*
X_{16} Foliar P		-----	0.33*	-0.15	- 0.38**	0.38**
X_{17} Foliar K			-----	-0.06	- 0.53**	0.33*
X_{18} Foliar Ca				-----	0.04	0.24*
X_{19} Foliar Mg					-----	-0.49**
Y Height increment (1961)	0.50**	0.44**	0.24*	0.02	- 0.33*	0.57**
r^2	25.00	19.36	5.76	0.04	10.89	32.49

[1] n = 100; df = 98; **significant at 1% level; *significant at 5% level.

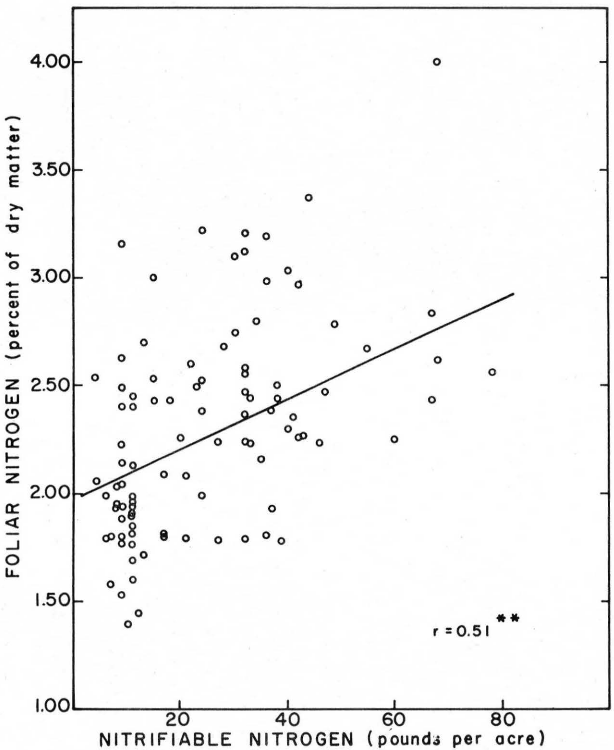

Figure 1. Relation between nitrogen in cottonwood leaves and nitrifiable nitrogen in the 0- to 6-inch layer of spoil material.

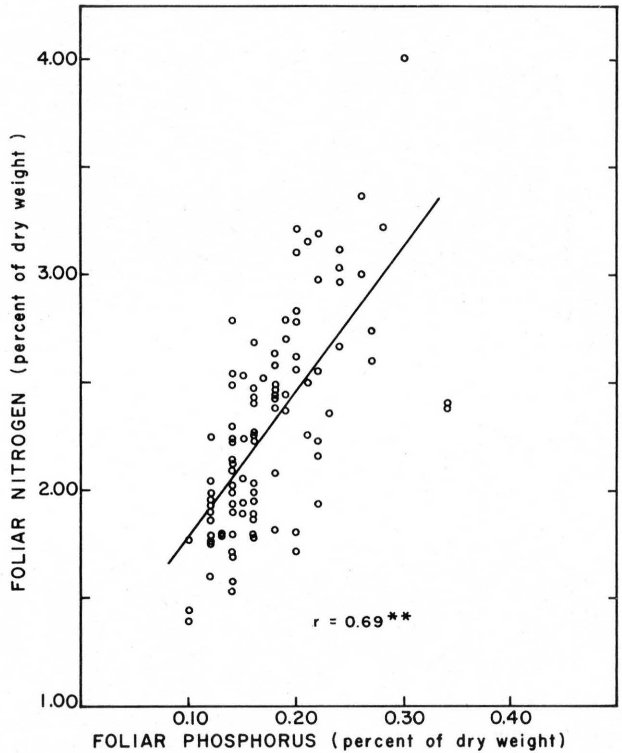

Figure 2. Relation between nitrogen and phosphorus in cottonwood leaves.

nitrogen was correlated. Moreover, he found that foliar nitrogen was correlated positively with cottonwood site index.

In studies of potted seedlings, Brendemuehl obtained a marked response to relatively high nitrogen levels when phosphorus was available in adequate quantities.

Linear Multiple Regressions

Tree age and nine chemical characteristics of the spoil materials accounted for approximately 49% of the variation in tree height. Tree age accounted for most of the variation; however, the coefficients for exchangeable and soluble calcium and soluble salt concentration were statistically significant (Table 4). Regression of tree height on the nine chemical characteristics reduced the variance 12% beyond that accounted for by age alone (Table 5).

Table 4--Multiple regression statistics for variables significant in the tree height - chemical characteristics regression, statistics adjusted for non-significant variables.

Y Total height		X_4 Exch. and soluble Ca	X_9 Soluble salts	X_{14} Tree age
$\bar{y}$ = 22.75	b_i	0.622*	-0.00283**	1.274**
	S_{b_i}	0.278	0.000895	0.227

**Significant at 1% level; *significant at 5% level.

The statistical significance of the coefficient for soluble salt concentration is interesting because simple correlation analysis indicated no relationship between soluble salts and tree height. A similar relationship, resulting from intercorrelation of variables, appeared in an earlier study (9). In the earlier study, high soluble salt concentrations were associated with both strongly acid and calcareous conditions. The present investigation, however, showed that soluble salt concentration was correlated with low pH, high exchangeable aluminum and high exchangeable hydrogen. The significant regression coefficient for soluble salts indicated that high salt concentrations were associated with decreased height growth not necessarily related to measures of coal-spoil acidity. Possibly, dissolved salts in acid coal-spoil conditions were toxic to tree roots.

Table 5--Analysis of variance of regression on nine deleted and one remaining variable for tree height.

Variation due to:	df	Sum of squares	Mean square
Regression on X_{14} (tree age)	1	1,816.60	1,816.60
Deviations	98	3,102.69	31.66
Total	99	4,919.29	
$F_{1,98} = 1,816.60/31.66 = 57.378^{**}$			
Regression on X_{14} (tree age)	1	1,816.60	1,816.60
Regression on X_1, X_2, X_3, X_4, X_6, X_7, X_8, X_9, X_{10} after fitting X_{14}	9	604.67	67.19
Regression on X_1, X_2, ..., X_{14}	10	2,421.27	242.13
Deviations	89	2,498.02	28.07
Total	99	4,919.29	
$F_{9,89} = 67.19/28.07 = 2.394^{*}$			

**Significant at 1% level; *significant at 5% level.

Linear multiple regression of tree height on three physical characteristics of the coal-spoil materials and tree age accounted for 47% of the variation in tree height. Coefficients for percentage of soil-size material and for tree age were significant (Table 6). The percentage of soil-size material probably reflects the nutrient status of spoil materials. In the range of conditions studied, physical characteristics of coal-spoil materials, as reflected by field capacity and air permeability at field capacity, seemingly did not limit cottonwood growth.

Table 6--Multiple regression statistics for variables significant in the tree height - physical characteristics regression, statistics adjusted for non-significant variables.

Y Total height		X_{13} <2-mm spoil	X_{14} Tree age
y = 22.75	b_i ⟶	0.487**	1.171**
	S_{b_i} ⟶	0.122	0.183

**Significant at 1% level.

A combined regression including seven chemical characteristics, percentage of soil-size material and tree age accounted for 52% of the variation in tree height. The statistically significant regression coefficients for soluble salts and soil-size material again indicated some relationship between growth of cottonwood and these measures of coal-spoil nutrient status (Table 7).

Table 7--Multiple regression statistics for variables significant in the tree height - combined characteristics regression, statistics adjusted for non-significant variables.

Y Total height		X_9 Soluble salts	X_{13} <2-mm spoil	X_{14} Tree age
$\bar{y}$ - 22.75	b_i ⟶	-0.00196*	0.382**	1.141**
	S_{b_i} ⟶	0.000799	0.136	0.202

**Significant at 1% level; *significant at 5% level.

Table 8--Multiple regression statistics for variables significant in the height increment - foliar nutrients regression, statistics adjusted for non-significant variables.

Y		X_{15}	X_{20}
Height increment		Foliar N	Initial tree height
$\bar{y} = 3.39$	b_i	1.614**	0.163**
	S_{b_i}	0.585	0.0364

**Significant at 1% level.

Table 9--Analysis of variance of regression on four deleted and two remaining variables for height increment.

Variation due to:	df	Sum of squares	Mean square
Regression on X_{15} (foliar nitrogen), X_{20} (initial height)	2	275.32	137.66
Deviations	97	376.52	3.88
Total	99	651.84	
$F_{2,97} = 137.66/3.88 = 35.479$**			
Regression on X_{15} (foliar nitrogen), X_{20} (initial height)	2	275.32	137.66
Regression on X_{16}, X_{17}, X_{18}, X_{19}, after fitting X_{15}, X_{20}	4	3.59	0.90
Regression on X_{15}, X_{16}, ..., X_{20}	6	278.91	46.48
Deviations	93	372.93	4.01
Total	99	651.84	
$F_{4,93} = 0.90/4.01 = 0.224$			

**Significant at 1% level.

Regression on initial tree height and foliar nitrogen, phosphorus, calcium and magnesium accounted for 43% of the variation in height increment during the 1961 growing season. Initial height and foliar nitrogen accounted for 42% of the variation, leaving a difference of 1% for the remainder (Tables 8 and 9). Relative concentrations of elements in the leaves probably are as important as the absolute concentrations of each element, and a regression including the interaction and quadratic terms of elements possibly would account for more variation in height increment.

In view of the results of correlation and regression analyses, deficiencies in available nitrogen and phosphorus in the coal-spoil materials may be the factors most limiting cottonwood growth. Conclusive evidence is not available from the results. Previous fertilizer experiments by Einspahr (4), however, indicated that phosphorus was the element first limiting plant growth on toxic, very acid and acid spoil materials, and that both nitrogen and phosphorus were deficient in loess and glacial till materials. Moreover, Brendemuehl (2), in a greenhouse study with cottonwood, demonstrated a good response to combined nitrogen and phosphorus fertilization.

CONCLUSIONS

In reference to the objectives of this study, the following were determined: 1) Growth of eastern cottonwood is related to the chemical characteristics of the coal-spoil materials. 2) A number of chemical factors are associated with cottonwood growth. 3) Data obtained can be used to formulate hypotheses for future controlled experiments designed to identify cause and effect relationships between chemical characteristics of the coal spoils and growth of cottonwood.

The variables best related to total tree height were soluble salt concentrate, exchangeable and soluble calcium and percentage of soil-size material. Leaf analyses, coal spoil analyses and current-year leader growth indicate nitrogen and phosphorus deficiencies.

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THE DEVELOPMENT OF MELOIDOGYNE HAPLA IN ALFALFA ROOTS UNDER CONTROLLED AND VARIABLE TEMPERATURES[1]

W. Arden Irvine[2]

ABSTRACT. Macroscopic and microscopic observations of healthy and *Meloidogyne hapla* infected alfalfa roots were made periodically for 28 and 30 days. Obvious swelling of alfalfa root tips occurred by the sixth day after seeding and infestation. Stained sections, however, showed that penetration by the nematodes had occurred by the fourth day. Penetration occurred most commonly at or near the root tip, but it was also observed to occur some distance behind the root tip although still within the region of active cell division.

Penetration and feeding by *M. hapla* in alfalfa roots produced the following macroscopic abnormal conditions: 1) development of large galls on the taproot and smaller galls on the lateral roots, 2) curvature of the root tip within five days after seeding, 3) proliferation of lateral roots in the galled areas, and 4) cessation of linear growth in some cases. Giant cells initiated from cells of the central cylinder and were first obvious as a group of cells with deep staining protoplasm. Later, these giant cells became obvious as multinucleate, large cells, in which the protoplasm stained lightly in some cases and darkly and granular in others. Vacuolation of the giant cells became evident early and was inversely correlated with the development of the nematode in that, by the time the nematode became an adult, the giant cells were almost devoid of protoplasm.

Egg production occurred within 28 days under variable temperatures. The life cycle of *M. hapla* progressed most rapidly in the following descending order of temperatures: 30°C>25°C>20°C>15°C. At 15° C the cycle proceeded slowly, with little apparent difference in development between six and 30 days. The severity of root-knotting, root-stunting, and lateral root proliferation was also in the order of 30°C>25°C>20°C>15°C.

In the variable temperature experiment, *M. hapla* caused significant reductions in yield at three months

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after seeding. At 30°C and 25°C the reductions in yield were significant at the 1% level. At 20°C the differences were significant at the 5% level, and at 15°C there was no significant difference in yield.

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INTRODUCTION

Most of the studies of host-parasite relationships with the root-knot nematode have been confined to studies on yield and to possible complexes between *Meloidogyne* and fungi and their effect on yield. Histological studies have been made only on sweet potato (17), tomato (2, 7, 21), gardenia (10), rose (11), soybean (8), and *Allium cepa* (26).

Invasion of the host tissue has been observed to occur at the root tip (3, 7, 14, 16, 20, 24, 27), in the region of cell elongation (19, 27, 24) and also through lateral root wounds and at mechanical breaks (17). Although various resting sites have been described, the most generally accepted final position of rest and feeding is in the plerom of the root (7, 10, 19).

One of the most obvious reactions of the host to the presence of root-knot nematodes is the production of galls. The galls produced may be characteristic of the root-knot species producing them; for example, those produced by *M. hapla* Chitwood, 1949, are smaller than those produced by *M. incognita incognita* (Kofoid and White, 1919) Chitwood, 1949, or *M. incognita acrita* Chitwood, 1949, on a given host. Lateral root proliferation is also a symptom resulting from infection by root-knot nematodes (7, 10, 22, 24). This may, however, depend on the species of *Meloidogyne* involved (25). Death of the root apical meristem because of penetration by large numbers of nematodes is common (7, 23). Microscopically, gall formation is the result of hypertrophy of cortical cells and cortical and stellar proliferation (7, 10).

Microscopically, one of the most common and outstanding features of galls is the presence of giant cells; these have been observed by a number of researchers (1, 2, 7, 8, 10, 11, 16, 17, 21, 26, 29). The fine structure of the giant cells in tomato has been studied in detail (2). Development of the giant cells involves coalescence of a number of cells at the feeding site, with the ultimate dissolution of the cell walls. This results in a large cell with thick walls and many nuclei which are often irregular in shape, greatly enlarged and contain many nucleoli. The cytoplasm is dense and granular and multivacuolate.

Penetration, survival and development of various *Meloidogyne* species in the presence and absence of various hosts have been studied (9, 12, 15, 30, 28). Most rapid completion of the life cycle appeared to occur at 27°C; however, penetration was observed to occur between 12°C and 35°C.

It has been found that 3000 and 1000 nematodes of *M. hapla* per half gallon of soil reduced the growth of alfalfa 58 and 42% in 175 and 381 days, respectively (4, 5, 6). Using 1000 juveniles in 500 gm of soil and comparing cut and uncut treatments, Chapman (4, 5, 6) found that the differences in top weights between treated and control plants were significant in both cut and uncut tests.

This presentation records determinations of the effect and development of Meloidogyne hapla Chitwood in alfalfa roots under variable and controlled temperatures.

MATERIALS AND METHODS

The Meloidogyne hapla culture used in all tests was originally obtained from dandelion roots in an alfalfa field in Story County, Iowa. Twenty-five hand-picked juveniles, obtained from a single dandelion gall, were rinsed in sterile water, and increased on tomato and subsequently on Ranger alfalfa in the greenhouse for several months prior to use. New populations were started from mass transfers from old cultures. The method of nematode extraction was adapted from Godfrey (13). When inoculum was desired, alfalfa plants were carefully removed from the soil, the roots were washed thoroughly, and galled lateral roots were placed on raised wire screens in petri plates. Enough distilled water was added to bathe but not submerge the roots. The juveniles which emerged from the roots were poured daily into a flask, and fresh water was added to the plates. If the nematodes were not used immediately, they were stored in an Erlenmeyer flask containing continuously aerated tap water. Storage varied from two - four days.

Variable temperatures were used in one experiment to study the effect of M. hapla on alfalfa roots. Steam sterilized soil in 6-inch clay pots was infested with 700 M. hapla juveniles, added to the soil in 5 cc of tap water. The nematodes were placed at the bottom of a hole, 2.5 cm diameter and 5 cm deep in the soil, in the center of the pot. Ranger alfalfa seeds were surface sterilized in a 27:1 dilution of Sephiran Chloride and rinsed in two changes of sterile distilled water. Ten seeds were placed 7 mm below the soil surface in each pot. After emergence, the seedlings were thinned to five per pot and were sectioned. Soil infestation and seedings were done on the same day.

A second test was similar to that described, except that constant-temperature tanks were employed. The soil temperatures were: 15°C, 20°C, 25°C, 30°C, with a variation of $\pm$ 1°C. One-quart plastic containers, painted on the outside with a semigloss black enamel, served as pots. The nematode inoculum was added to the soil as described previously, except that 1200 - 1300 nematodes were placed at the bottom of a hole 6.5 - 7.5 cm deep. There were five alfalfa plants per pot.

In the first experiment, roots were gently removed daily, from the third to the twelfth day after seeding, and examined for galls. Thereafter, sampling was extended to 4-day intervals up to and including 28 days after seeding. Samples for sectioning were taken at 2 months. In the controlled-temperature experiment, roots for sectioning were soaked gently out of the containers at 6-day intervals for 30 days after seeding.

Root measurements of the tap roots were made up to 20 days after seeding. Measurements were not made after this since the roots became too branched in the galled areas to distinguish the tap from the lateral roots.

Root pieces for sectioning were killed and fixed in Craf III, dehydrated and prepared for embedding in wax by the ethyl-alcohol method of Sass (23). The pieces of tap root used for sectioning were taken along the root at measured intervals from the base of the cotyledons. Lateral roots below the 5 cm depth in the soil were also sectioned. Depending on the age and woodiness of the material, sections were cut at a thickness of 10 or 12 μ on a rotary microtome. The sections were stained with safranin and fast green.

Corresponding experiments were set up in which yield data was recorded. The same number of nematodes, temperatures and alfalfa plants were used as previously described. In the variable-temperature experiment, five replications were used. The first cutting was made at 2 months and at monthly intervals thereafter, up to 8 months. In the constant-temperature tanks, six replications were used, with the first cutting being made at eight weeks and at 4-week intervals thereafter, up to 20 weeks. Dry weights of the tops were recorded at each cutting. At the conclusion of these experiments, the dry weights of the roots were also recorded.

RESULTS

Macroscopic Appearance of Roots

Experiment at variable temperatures

Although penetration of *Meloidogyne hapla* had occurred by the fourth day, obvious swelling of infected root tips did not occur until the sixth day after seeding. Infected root tips were observed to curve within 5-10 days after seeding (Fig. 1). In some cases, there was only a slight curvature, while in others, the root formed a complete circle. By 8 days after seeding, numerous lateral roots had emerged from the taproot, and these laterals had swollen tips, indicating nematode penetration (Fig. 1). Lateral roots arose close to the infected taproot tip. By 10 days, the lateral roots were severely galled. This swelling of the lateral root tips was particularly evident at approximately the 5 cm depth in the soil. Some of the taproot tips of check plants were also swollen, but this is a common phenomenon when roots reach the bottom of a pot as occurred here (Fig. 1).

Slowing and cessation of linear root growth in the *M. hapla* treatments was evident early, as indicated by the root length measurements taken at 3-20 days, Table 1. Lateral root development, on the other hand, was much greater on the nematode-invaded roots than on the noninvaded roots. The number of lateral roots arising from a galled area on the taproot varied from one to twelve, except in one instance in which approximately 20 were observed. The lateral roots of the check plants were fibrous, whereas those from the nematode-invaded plants were much thicker. The knots were usually larger on the tap than on the lateral roots. The bunchy appearance of the infected roots at 16 and 20 days made it difficult to measure root lengths. For this reason, little emphasis should be placed on the measurements taken at 16 and 20 days.

Bacterial nodules were not evident until approximately 28 days after seeding.

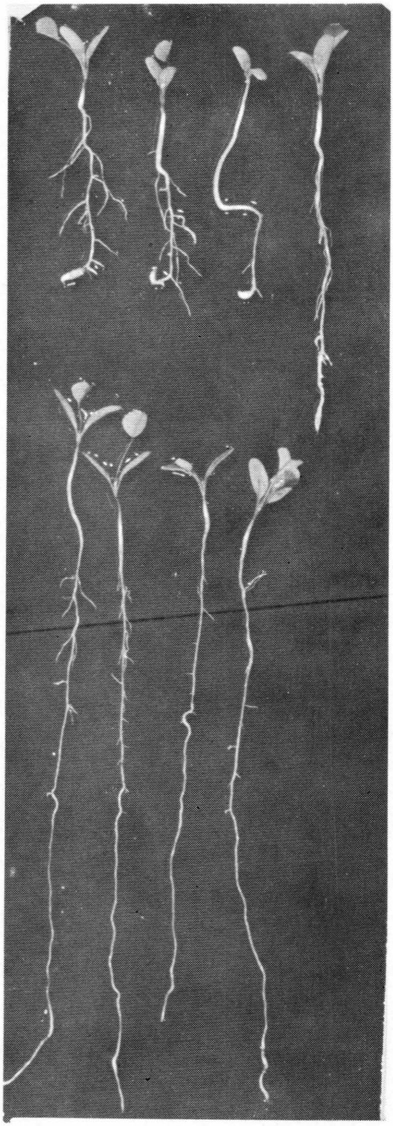

Figure 1. 'Ranger' alfalfa roots 8 days after seeding and inoculation. Note the swelling and curvature at the tip of the tap root of nematode treatments—top, and nonnematode treatments—bottom.

Table 1. Alfalfa root lengths up to 20 days after planting seed in soil infested with Meloidogyne hapla.

Days After Planting	Inoculated Plants (cm)	Check Plants (cm)
3	4.1	3.7
4	5.6	6.2
5	5.0	7.0
6	5.0	8.5
7	5.0	12.5
8	5.3	13.5
9	5.8	12.7
10	7.1	14.7
11	4.8	14.7
12	5.7	20.3
16	5.1	18.0
20	12.5	19.1

Experiment at controlled temperatures

Macroscopic examination of the roots from the temperature tanks revealed approximately the same results as those from the previously described bench experiment, especially at soil temperatures 20°C, 25°C and 30°C. Swollen and curved root tips occurred at 6 days after seeding at all temperatures except 15°C, at which plant growth was much slower. Plants in infested soil had swollen root tips at all four temperatures by 12 days.

The severity of root-knotting and root-stunting was in the order of 30°C>25°C>20°C>15°C at 24 and 30 days after seeding. There were fewer knots with less lateral root proliferation at 15°C. Root growth in non-infested soil was greatest at 25°C and 20°C. Top growth was greater at 25°C and 20°C than at 30°C and 15°C at 24 days after seeding. At 30 days, knots were usually larger on the tap than on lateral roots.

Microscopic Appearance of Roots

Experiment at variable temperature

Root knot nematodes were first observed in the root tip sections 4 days after seeding, which probably was the first day of nematode contact with the roots.

Penetration by second-stage juveniles was observed to occur most commonly directly through the root cap and tip, and behind the root tip but in the region of the meristematic zone (Fig. 2). No penetration was observed to occur at lateral root ruptures.

Nematodes were observed in or at the edge of the plerome within 5 to 6 days after seeding (Fig. 3, 4). At 6 days, nematodes were observed in the terminal 0.5 cm and in the 0.5-1.0 cm piece behind the root tip. By

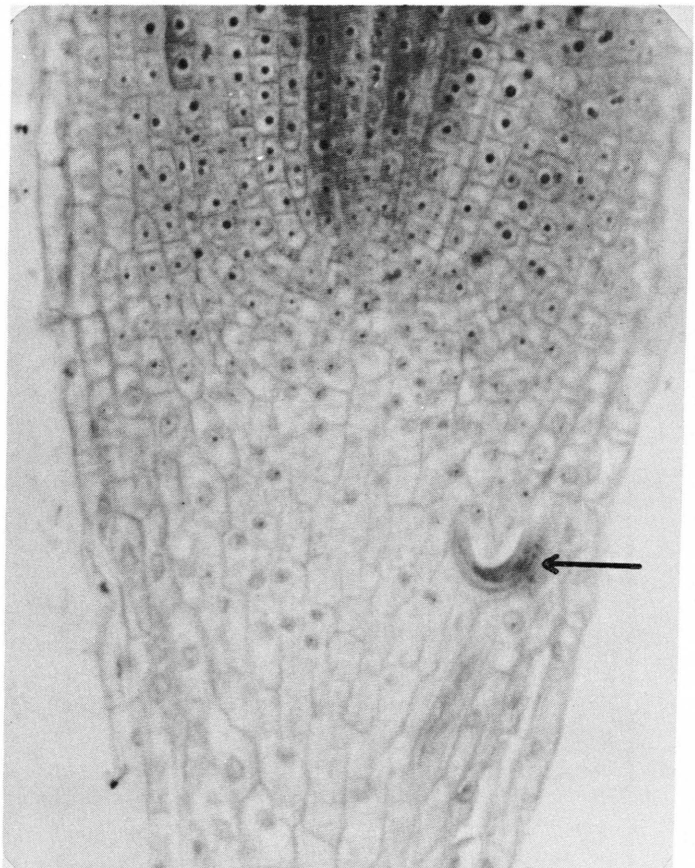

Figure 2. Meloidogyne hapla juvenile in the root cap 5 days after seeding. (400 x)

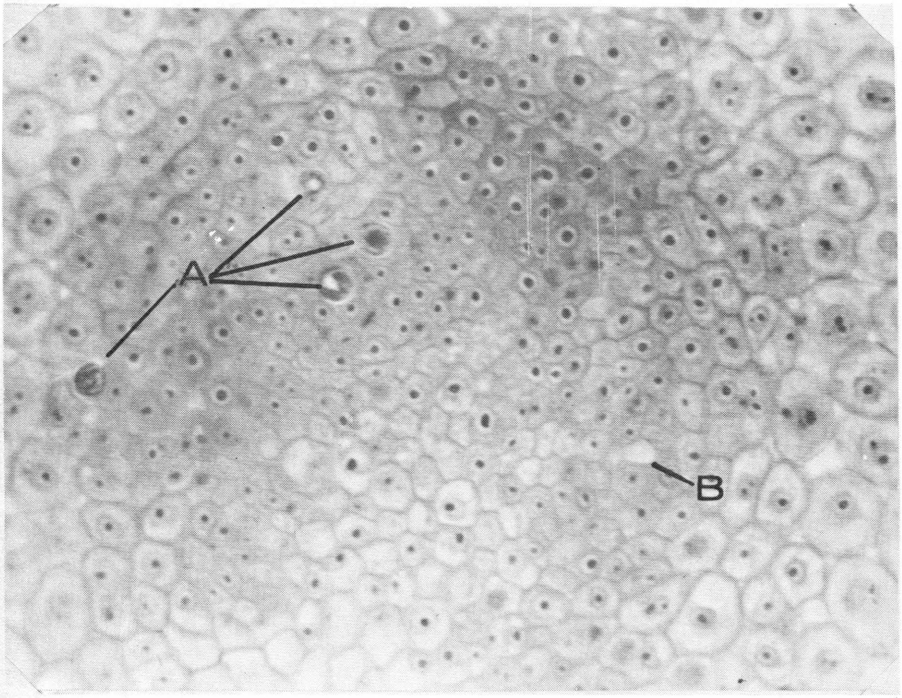

Figure 3. Cross-section of juveniles of M. hapla in the plerome at 6 days after seeding (400x).
A = nematodes. B = protophloem cell.

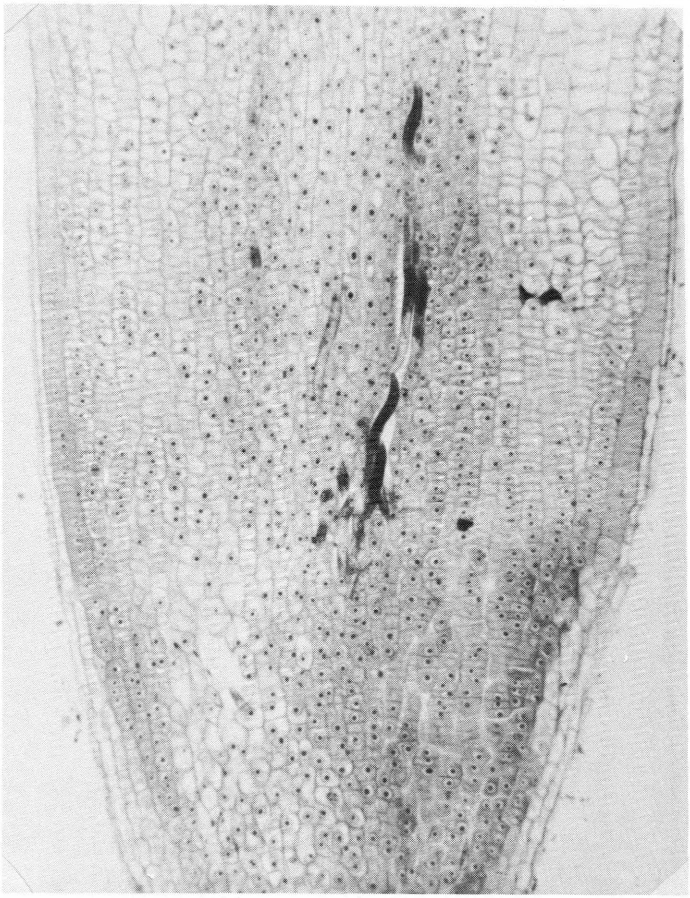

Figure 4. Several juveniles in the plerome at 6 days after seeding. (180 x)

7 days, individual nematodes were observed in the central cylinder in the second cm from the tip and, later, occasionally in the third cm from the root tip. Occasionally, the posterior end of the nematode extended into the cortex, and on occasion, the nematode was entirely in the cortex. In this latter case, evidence of feeding on the cells and the production of giant cells was not observed.

Mass as well as individual penetration by the nematodes occurred (Fig. 4). In the former case, an obvious path of entry was present, but in the latter case, tunneling was not as evident, although the nematodes were intercellular in the plerome. Ultimately, the nematodes came to rest and began feeding in the central cylinder.

The root curvature, observed macroscopically resulted when several nematodes invaded the root tip, usually to one side of the tip. The curvature was due to a suppression of growth at the site of invasion. The degree of curvature produced was slight to very severe (Figs. 5, 6).

The root cap of infected roots was not as well developed as that of noninfected roots.

Macroscopically, the knotted areas of the roots showed great proliferation of lateral roots. Sections of these areas contained, in practically every case, a nematode or giant cells, or both, in the area of the origin of the lateral root (Fig. 7). In roots 6 days old or older, lateral root proliferation, with nematodes and giant cells at the base, frequently occurred close to the root tip as well as farther back. The presence of the nematode appeared to have stimulated lateral root initiation. This lateral root initiation can probably be incited by both males and females, although females were predominant at the base of the laterals.

After penetration had occurred and feeding had begun, the ultimate effects of presence of nematodes on the host cells were hypertrophy and the production of giant cells. In the stele, the giant cells began to form at approximately 6 days after seeding. An area in which giant cells were developing first became evident as a group of cells with dark-staining protoplasm. Some cases were observed, however, in which the protoplasm stained lightly at first. The cells in this area undergo mitotic division. It is thought, however, that no cross walls form between the daughter nuclei (Fig. 8). No nuclear divisions were observed in the older giant cells, approximately 20 through 30 days. The giant cells were multinucleate, and the nuclei were usually multinucleolate, whereas normal cells generally only had one nucleolus. In the multinucleolate nucleus, the nucleoli were very small. The nuclei were often large and usually irregularly shaped.

Abnormal conditions were observed which may help in explaining the large, irregular nuclei and multinucleolate condition in dividing cells of infected roots. These dividing cells were observed to contain chromosomes and nucleoli which lagged behind, while the remainder of the chromosomes were lined up across the center of the cell in the metaphase stage of division. The presence of nucleoli at this stage is unusual since, under normal conditions, the nucleoli have disappeared prior to this phase of division. However, nematodes were not observed to feed on any of these cells, and, it is not certain if these conditions were due to nematode presence or just due to abnormality of the cells themselves.

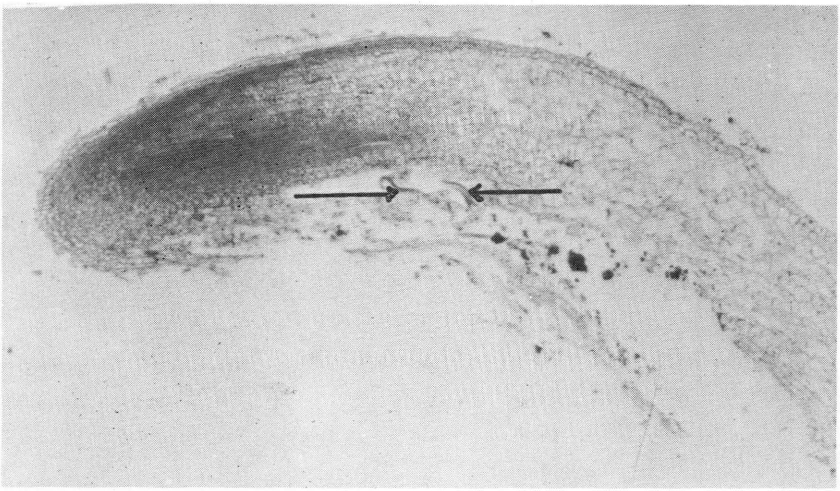

Figure 5. Longitudinal section showing curvature of the root at the tip 6 days after seeding (60x). Arrows point to nematodes.

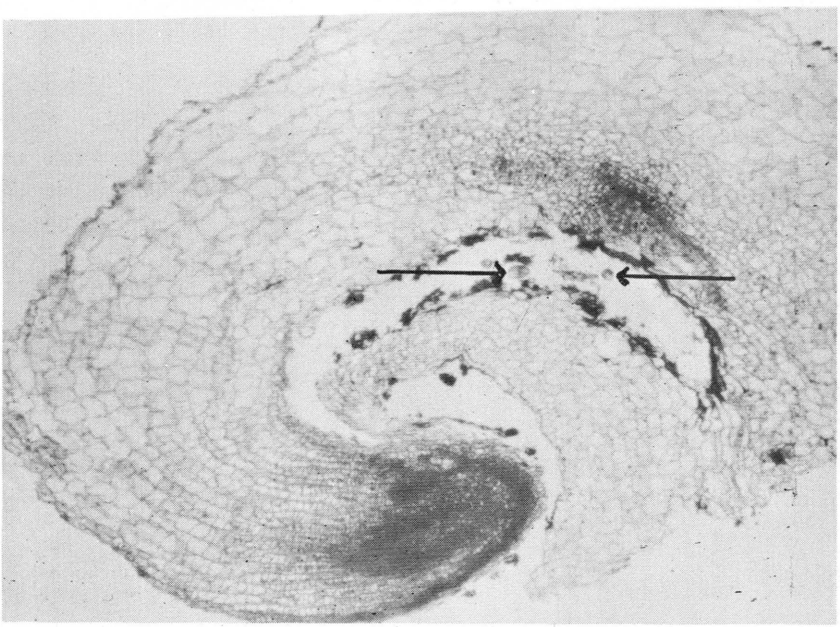

Figure 6. Longitudinal section of Ranger alfalfa showing the severity of curvature of the root at 9 days after seeding (60x). Arrows indicate nematodes.

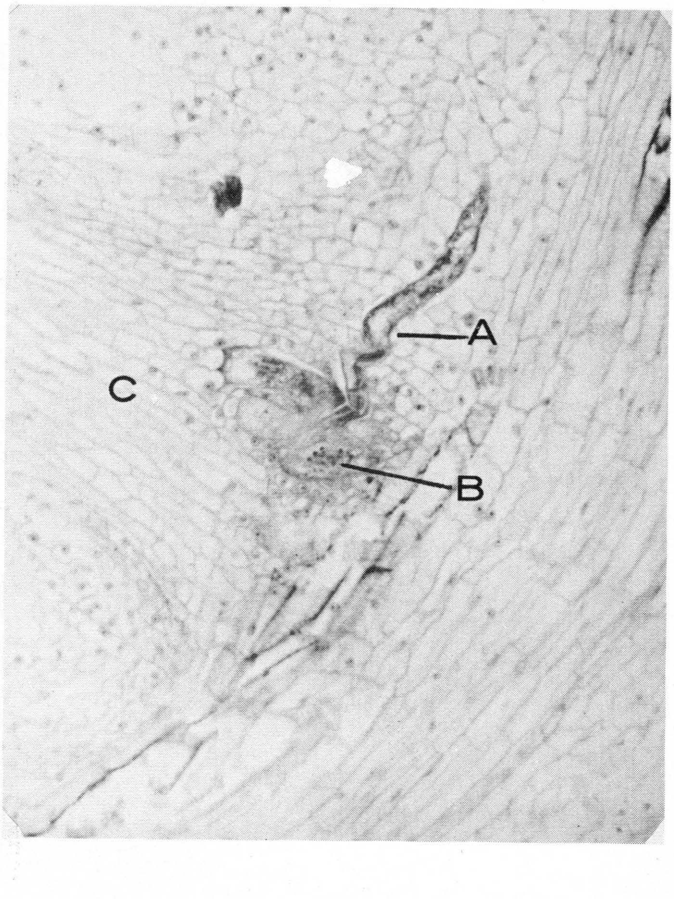

Figure 7. Multinucleate giant cells with deep staining, granular protoplasm and vacuoles at the base of a lateral root 11 days after seeding (160x). A = nematode, B = multinucleate giant cells, C = lateral root.

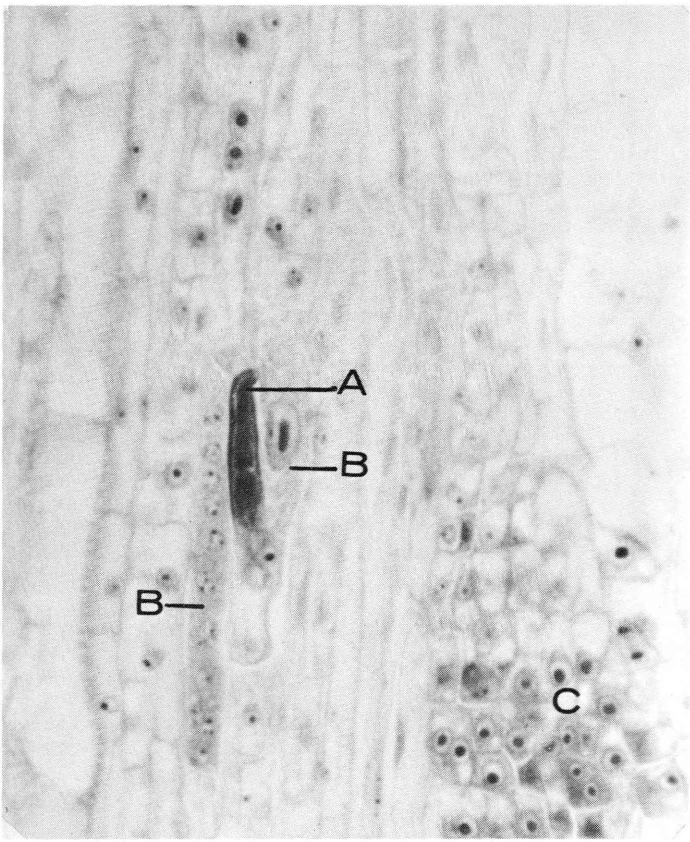

Figure 8. Beginning of giant cell production in the vascular tissue, 6 days after seeding (400x). A = nematode, B = giant cells. Note no crosswalls evident and also the multinucleolate situation and the large nucleus with irregular nucleolus, C = lateral root beginning.

Vacuolation of the giant cells became evident early after their formation. Each giant cell contained a number of vacuoles (Fig. 7). This vacuolation increased so, that by the time the nematode was an adult, there was very little protoplasm left in the cell (Figs. 9, 10). In these cells, there was usually a deep-blue-staining area which contained numerous small, red-staining bodies which were probably nucleoli. The large number of nucleoli may indicate the coalescence of nuclei and the beginning of deterioration of the nuclei. Not all giant cells in a root section were in the same stage of development. There were usually three to five, and in some cases more, giant cells around the anterior end of the nematode. The effect of the giant cells on the vascular tissue was interruption and displacement of the vascular elements (Fig. 9).

By 20 days after seeding, the female nematode was pear-shaped, and a vulva was evident. A molted cuticle was not seen until 24 to 28 days after seeding. Between 20 and 28 days after seeding, the giant cells gradually became more vacuolate, and at 28 days, these cells were practically devoid of protoplasm.

In the variable-temperature experiments, the egg sac of the female contained eggs by 28 days after seeding. In the constant-temperature tanks, the rapidity of development of the nematodes was in the descending order of 30°C, 25°C, 20°C, 15°C, with the eggs first appearing in the roots at 30 days in the 30°C tank. Eggs were not present by this time at any of the other temperatures. The nematodes in the root sections from the 15°C tank showed very little progress in development between 6 and 30 days after seeding.

Yield Data

Significant differences in yield were evident at 3 months after seeding in the variable-temperature experiment (Table 2). This trend continued until 8 months, at which time no significant differences were observed between the two treatments. At the conclusion of this experiment, the

Table 2. Dry weights in gms of the top growth of alfalfa. Average of five replications for a period of 8 months. Variable temperature.

Time in Months	Top Weights (gms) Nematode treated	Check
2	4.38	4.73
3	4.42	5.44
4	2.56	4.88
5	2.13	3.95
6	2.94	3.98
7	2.04	3.76
8	1.65	2.35

L.S.D. at .05 = 1.981
L.S.D. at .01 = 2.621

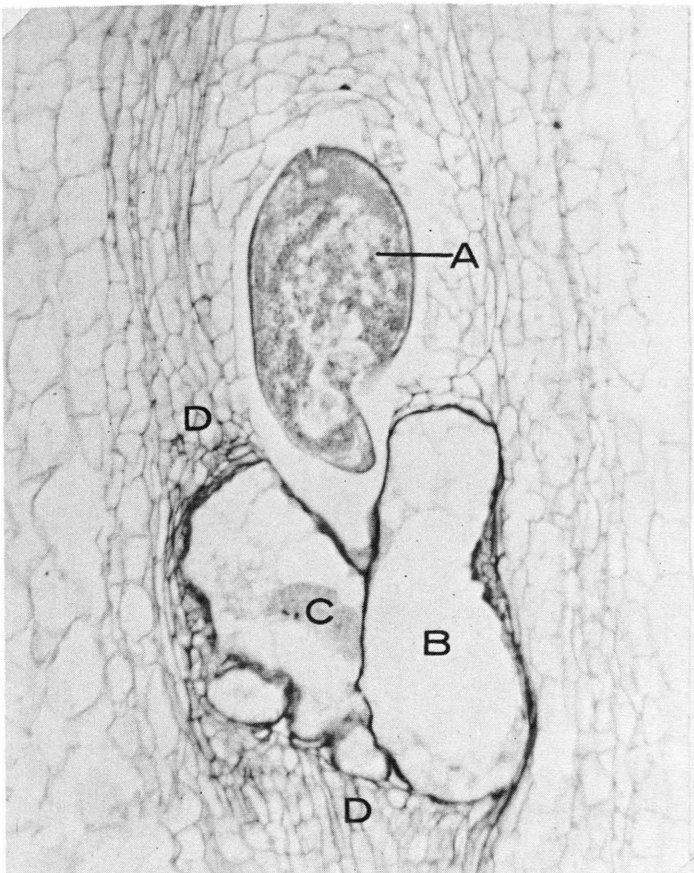

Figure 9. Obese female showing vulva and nearly empty giant cells at 20 days after seeding (160x). (Note interruption of xylem vessels by the giant cells at D.) A = nematode, B = giant cells, C = coalesced nuclei in the giant cell. The nuclei have begun to deteriorate and break down.

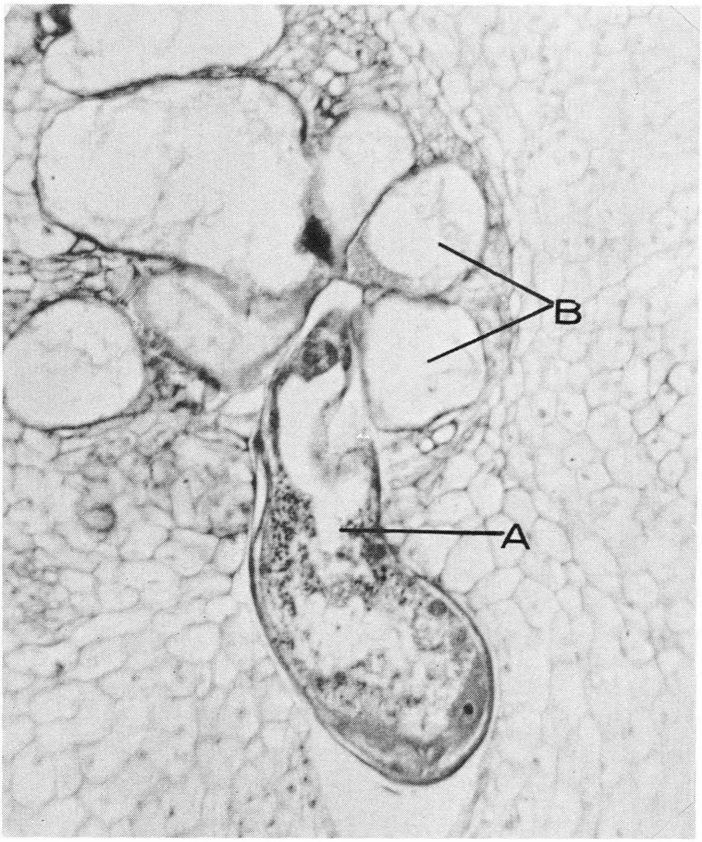

Figure 10. Large female nematode with large giant cells devoid of protoplasm at 24 days after seeding (160x). A = nematode, B = giant cell with very little protoplasm.

dry weights of the roots exhibited the same weight pattern as the dry weights of the tops (Table 3).

Flowering did not follow a set pattern. When flowering did occur, however, the check plants usually flowered first, producing the largest and most abundant blooms.

In the temperature-tank experiment, the first cutting of the tops was made at 8 weeks after seeding. The dry-weight data averages for each cutting are presented in Table 4. At 8 weeks, the lowest weights occurred in the nematode treatments, with these differences being greatest at 30°C and 25°C. At 20 weeks in these temperatures, the plants in the nematode treatments were only approximately half those of the check plants.

Using the Duncan Multiple Range Test, calculated on treatment means at each temperature, difference in dry weights between treatments were not significant at 15°C. At 20°C, significant differences at the 5% level were evident between the treatments. At 25°C and 30°C, the dry weight differences between the nematode and check treatments was significant at the 1% level (Table 4).

At the conclusion of the constant temperature experiment, the dry weights of the roots showed a pattern similar to that of the dry weights of the tops in that the root-knot infected roots weighed less than those of the check plants (Table 5). This was especially evident at 20°C, 25°C, and 30 C. Also, as shown by root-knot indexes, the severity of root galling was in the order of 30°C>25°C>20°C>15°C.

DISCUSSION

The results presented here are in general agreement with those found by other workers on other hosts. Some points of difference, however, will be discussed.

Christie (7) stated that, "As time goes on, the protoplasmic network usually becomes denser and the spaces smaller until, at the end of 30 to 40 days, they are more nearly homogeneous in nature." In the serial sections of alfalfa roots, the giant cell development advanced from a multinucleate condition, with abundant granular protoplasm with many small vacuoles when the juvenile was present, to one in which the cells were large and practically devoid of protoplasm as the nematode approached maturity at approximately 20 to 28 days. This gradual breakdown of the protoplasm seems reasonable because of the multivacuoles in the young giant cells and also since the nematodes, during their sedentary existence in the root, feed on these giant cells.

In the early formation of the giant cells, it appears that the cells fed upon divide, but no cross walls apparently formed between the daughter cells, thus giving a multinucleate condition. This would probably account for the large number of giant cells around the head end of the nematode. No division of the nuclei in the older giant cells, 20 through 30 days, was observed, and thus, the giant cells probably reached their ultimate size early in their development.

The nuclei in cells on which the nematodes fed were large and irregular (Fig. 8). This abnormal condition could possibly be due to an increase in chromosome number, although chromosomes were not counted, or to

Table 3. Dry weight of the roots in gms at the end of the eight month period. Variable temperatures.

Time Months	Root Weights (gms) Nematode Treated	Check
8	4.63	13.14

Table 4. Dry weights of the tops at four cuttings and four temperatures for a period of 20 weeks. Average of six replications.

		Dry Weight Tops (gms)			
Treatment	(wks)	15°C	20°C	25°C	30°C
Nematode	8	1.59	1.57	1.18	0.48
	12	1.63	1.59	1.30	0.78
	16	1.85	1.64	1.33	0.94
	20	2.11	1.87	1.73	1.02
Check	8	1.78	1.70	1.29	0.78
	12	1.59	1.86	1.41	1.00
	16	1.85	2.21	1.94	1.36
	20	2.44	2.69	3.01	2.17

Significance levels for the overall treatment means at each temperature as shown by the Duncan Multiple Range Test were: 15°C - N.S.: 20°C - 5%; 25°C - 1%; 30°C - 1%.

Table 5. Dry weights of the roots in gms after 20 weeks at four temperatures.

	Dry Weight Roots (gms)			
Treatment	15°C	20°C	25°C	30°C
Nematode	2.72	2.80	2.17	1.46
Check	3.05	5.12	4.78	3.63

coalescence of a number of nuclei. Owens and Specht (21) suggest nuclear enlargement in the early stage to be due to swelling. The multinucleolate conditions of the nuclei could be due to the lagging behind of nucleoli at division of the nucleus. This possible lag condition in nematode-treated roots was observed in two cases. Nematodes were not observed to feed on these cells, however. Owens and Specht (21), on the other hand, suggest occurrence of nucleolar fragmentation, which is in accord with the smaller size of the nucleoli in the nuclei of the giant cells.

The profusion of lateral roots in conjunction with galls induced by *M. hapla* has been observed in alfalfa (22), but no histological study was made. In the present histological study, a nematode was found in nearly every case, at the base of a lateral root arising from a galled area. This phenomenon of lateral root stimulation is difficult to explain, especially since these same nematodes will often cause the cessation of linear growth. Since lateral roots were often observed to arise extremely close to the root tip, there may be some phenomenon involved which hastens the maturity of the meristematic tissue.

The most rapid completion of the life cycle of *M. hapla* was at 30° C. This is in close agreement with results found by Tyler (30) for what was then called *Heterodera marioni*.

The fact that *M. hapla* develops readily in alfalfa, especially at warmer temperatures, was shown by both the histological study and the yield study. In the variable temperature experiment the lack of significance at 8 months was probably due to pot binding and a depletion of nutrients in the check pots.

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THEORY OF THE SOLUBILITY OF PHOSPHATE ROCK[1]

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ABSTRACT. The principal phosphatic component of most phosphate rocks is probably hydroxyfluorapatite. Hydroxyfluorapatite is the name given to mineral species in an isomorphous series of compounds intermediate in composition between fluorapatite and hydroxyapatite. The solubility of phosphate rock is considered from the standpoint of solubility-product constants with a view to setting forth a theoretical basis for examining the solubility behavior of phosphate rock in soil solutions. Topics covered include activities of phosphate ions, activities of calcium and other ions, diagrammatic representation of solubility relations of calcium phosphates, solubility of hydroxyapatite, solubility of fluorapatite, and solubility of hydroxyfluorapatite.

INTRODUCTION

The first step in utilization by plants of the phosphorus applied to soil as phosphate rock probably is the partial dissolution of the phosphate rock. The dissolved phosphorus then may move directly through the soil solution to the root surface, where it is absorbed. Alternatively, the phosphorus released from the phosphate rock may disappear temporarily into the solid phase of the soil, reappearing in solution at a later time and being absorbed by plants.

Factors that may affect the rate at which phosphorus is transferred from phosphate rock to plant root or to soil solid phase include (a) the rate at which the phosphorus can appear in solution from the phosphate rock, (b) the concentration of phosphorus in the saturated solution, (c) the rate at which the phosphorus can be removed from solution, and (d) the conditions of transport between source and destination. There is no doubt that some significant limitation exists because undissolved phosphate rock has been found in soil years after application (Fine and Bar-

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tholomew, 1946) and because plants growing on soils treated with phosphate rock rarely, if ever, have phosphorus percentages as high as those that would be found if phosphorus were being absorbed from a culture solution at the maximum rate attainable by increasing the concentration.

Work by Stelly[3], Fried et al. (1957), Honert (1933), and others suggests that both the rate of solution of phosphate rock and the concentration of phosphorus in a saturated solution of phosphate rock in water are adequate to maintain the rate of absorption of phosphorus by plants near the maximum. The failure of plants to absorb phosphorus at such a rate from soils treated with phosphate rock has never been explained in satisfactory detail, but conditions related to b and d of the preceding paragraph may be contributory. With regard to b, it may be suggested that common ions present in the soil solution cause the concentration of phosphorus in the film of solution around phosphate rock particles to be below that obtained where phosphate rock is equilibrated with water adjusted to the same pH value as that of the soil by addition of hydrochloric acid or sodium hydroxide. With regard to d, it may be suggested that dissolution of the phosphate rock causes the soil solution to become supersaturated with respect to other phosphate compounds or adsorption complexes, so that phosphorus is withdrawn continuously from the diffusion stream leading away from the particles, and the condition of saturation that presumably exists at the surface of the phosphate rock extends only a short distance outward into the surrounding soil. As perhaps secondary but nevertheless significant conditions related to transport, one may mention also the proportion of the soil volume through which transport can occur, i. e., the proportion of the soil volume occupied by water, and the tortuosity of the diffusion pathway.

The preceding paragraph deals with the negative aspects of the problem. From the positive standpoint, the activity of hydrogen ions in the solution bathing the particles of phosphate rock is known to have a profound effect on the solubility of the phosphorus because of the strong tendency of hydrogen ions to associate with PO_4^{---} and HPO_4^{--}. The buffering capacity of soil provides a means of sustaining the supply of hydrogen ions over a long period of time.

Because pronounced differences among soils are known to exist as regards the activity of hydrogen and other ions, there is reason to think that the solubility of phosphate rock may show corresponding differences in these soils. Hence an examination of the solubility behavior of phosphate rock appears to be a reasonable point of departure in investigating the utilization of the phosphorus of phosphate rock by plants.

The purpose of this paper is to describe the theoretical background for solubility measurements on phosphate rock. The paper will treat first the subject of ion activities, with particular reference to the several orthophosphate anions and to other ions of significance in work on the solubility of phosphate rock and calcium phosphates in general. Solubility relationships of hydroxyapatite and fluorapatite will then be considered. These mineral species are end-members of a series of solid solutions

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[3] Stelly, Matthias. 1942. Forms of inorganic phosphorus in the lower horizons of some Iowa soils as indicated by plant availability and chemical methods. Ph. D. Thesis, Iowa State College.

of hydroxyfluorapatite, which is thought to be the principal phosphatic constituent in most phosphate rock. With the foregoing background, the solubility relationships of hydroxyfluorapatite will then be discussed.

The ion-product approach described here is not original with the authors. It represents an application of well-known principles of chemistry. Various other investigators, including Eriksson (1952), Aslyng (1954), Clark and Peech (1955, 1960), Cole and Olsen (1959a, 1959b), Lindsay and Moreno (1960), Lindsay, Peech, and Clark (1959a, 1959b), Olsen, Watanabe, and Cole (1960), and others, have applied these principles in investigations of phosphates in soil. Their applications have been different from the present one. But because all such applications have elements in common, and because previous treatments of the theory have been synoptic in nature, the contents of the present paper may be of some value not only to those interested in the particular problem under consideration but also to those interested in allied problems.

Activities of Phosphate Ions

In solutions that are sufficiently dilute, the activities of ions are numerically equal to the molar concentrations. In more concentrated solutions, the activity of each ionic species is equal to the product of the activity coefficient and molar concentration of the ion.

Although inorganic orthophosphate exists in several forms in solution, viz., H_3PO_4, $H_2PO_4^-$, HPO_4^{--}, and PO_4^{---}, methods of analytical measurement of phosphorus make no distinction among forms and provide only a measure of the total phosphorus. The activity of individual species is calculated with the aid of additional information, as indicated below.

The phosphorus-conservation equation requires that

$$(P_T) = (H_3PO_4) + (H_2PO_4^-) + (HPO_4^{--}) + (PO_4^{---}), \tag{1}$$

where the brackets indicate molar concentrations, and P_T stands for the total orthophosphate-P measured analytically.

The activity expressions for the various phosphate forms are

$$a_{H_3PO_4} = \gamma_{H_3PO_4} \times (H_3PO_4), \tag{2}$$

$$a_{H_2PO_4-} = \gamma_{H_2PO_4-} \times (H_2PO_4-), \tag{3}$$

$$a_{HPO_4--} = \gamma_{HPO_4--} \times (HPO_4^{--}), \tag{4}$$

and

$$a_{PO_4---} = \gamma_{PO_4---} \times (PO_4^{---}), \tag{5}$$

where the γ's represent the activity coefficients and the a's stand for the activities of the respective phosphate forms. Equation 1 can be written in terms of activity and activity coefficients by substituting 2, 3, 4, and 5 into it to obtain

$$(P_T) = \frac{a_{H_3PO_4}}{\gamma_{H_3PO_4}} + \frac{a_{H_2PO_4^-}}{\gamma_{H_2PO_4^-}} + \frac{a_{HPO_4^{--}}}{\gamma_{HPO_4^{--}}} + \frac{a_{PO_4^{---}}}{\gamma_{PO_4^{---}}}. \tag{6}$$

The three dissociation expressions of orthophosphoric acid may be written as

$$\frac{a_{H_2PO_4^-} \times a_{H^+}}{a_{H_3PO_4}} = K_1, \tag{7}$$

$$\frac{a_{HPO_4^{--}} \times a_{H^+}}{a_{H_2PO_4^-}} = K_2, \tag{8}$$

and

$$\frac{a_{PO_4^{---}} \times a_{H^+}}{a_{HPO_4^{--}}} = K_3. \tag{9}$$

Combining and solving these expressions in terms of one particular phosphate species and substituting the resulting expressions into 6 gives a new expression for the total phosphorus concentration (P_T) in terms of that particular phosphate form, the hydrogen-ion activity, the various activity coefficients, and the three dissociation constants. For instance, combining and solving 7, 8, and 9 in terms of $a_{H_2PO_4^-}$ and substituting the resulting expressions into 6 yields

$$(P_T) = a_{H_2PO_4^-} \times \left\{ \frac{a_{H^+}}{K_1 \gamma_{H_3PO_4}} + \frac{1}{\gamma_{H_2PO_4^-}} + \frac{K_2}{a_{H^+}\gamma_{HPO_4^{--}}} + \frac{K_2K_3}{a_{H^+}^2 \gamma_{PO_4^{---}}} \right\} \tag{10}$$

Two analogous expressions can be obtained when equations 7, 8, and 9 are combined and solved for $a_{HPO_4^{--}}$ and for $a_{PO_4^{---}}$.

An immediate consequence of the validity of the dissociation expressions of phosphoric acid and of the numerical values of the constants K_1, K_2, and K_3 is that, for a given total phosphorus concentration, a particular pH range exists, different for each phosphate species, in which a particular species predominates over the others present at that pH. Furthermore, functions can be found which express the ratio of the total phosphorus concentration, determined analytically, to the activity of each phosphate species. Each ratio is a function of the pH of the solution and the various activity coefficients (or, of the pH and the ionic strength) of the solution. One such function is obtained by dividing equation 10 by $a_{H_2PO_4^-}$.

The activity coefficients of the phosphate ions may be estimated from the Debye-Hückel formula,

$$\log \gamma_i = \frac{-A\, z_i^2\, (\tfrac{1}{2}\Sigma c_i z_i^2)^{1/2}}{1 + 10^8 a_i\, B\, (\tfrac{1}{2}\Sigma c_i z_i^2)^{1/2}}, \tag{11}$$

where γ_i, c_i, and z_i are the activity coefficient, concentration, and valence of the i'th ionic constituent; A = 0.5092; B = 0.3286; and the values of $10^8 a_i$ are those given by Kielland (1937), namely, 4 for HPO_4^{--}, 4.25 for $H_2PO_4^-$, and 4 for PO_4^{---}. Use of formula 11 implies a value of 1 for $\gamma_{H_3PO_4}$. The expression $(\frac{1}{2}\Sigma c_i z_i^2)$ is called the ionic strength and is usually denoted by μ. The summation is carried out over all ions present in the solution.

In the following, $f_1(pH)$ will designate the ratio of the total phosphorus concentration to the activity of $H_2PO_4^-$; $f_2(pH)$, the ratio of the total phosphorus concentration to the activity of HPO_4^{--}; and $f_3(pH)$, the ratio of the total phosphorus concentration to the activity of PO_4^{---}.

The functional dependence of these ratios on the activity of hydrogen ions, the activity of coefficients of the phosph species, and the three dissociation constants of phosphoric acid, K_1, K_2, and K_3, is given by

$$f_1(pH) = \frac{(P_T)}{a_{H_2PO_4^-}} = \frac{a_{H^+}}{K_1} + \frac{1}{\gamma_{H_2PO_4^-}} + \frac{K_2}{a_{H^+}\gamma_{HPO_4^{--}}} + \frac{K_2K_3}{a_{H^+}^2\gamma_{PO_4^{---}}}, \tag{12}$$

$$f_2(pH) = \frac{(P_T)}{a_{HPO_4^{--}}} = \frac{a_{H^+}^2}{K_1K_2} + \frac{a_{H^+}}{K_2\gamma_{H_2PO_4^-}} + \frac{1}{\gamma_{HPO_4^{--}}} + \frac{K_3}{a_{H^+}\gamma_{PO_4^{---}}}, \tag{13}$$

and

$$f_3(pH) = \frac{(P_T)}{a_{PO_4^{---}}} = \frac{a_{H^+}^3}{K_1K_2K_3} + \frac{a_{H^+}^2}{K_2K_3\gamma_{H_2PO_4^-}} + \frac{a_{H^+}}{K_3\gamma_{HPO_4^{--}}} + \frac{1}{\gamma_{PO_4^{---}}}. \tag{14}$$

Multiplication of $f_1(pH)$ by $\frac{a_{H^+}}{K_2}$ yields $f_2(pH)$, and multiplication of $f_2(pH)$ by $\frac{a_{H^+}}{K_3}$ yields $f_3(pH)$, in agreement with equations 8 and 9, wherefrom

$$f_2(pH) = \frac{(P_T)}{a_{HPO_4^-}} = \frac{a_{H^+}}{K_2} \times \frac{(P_T)}{a_{H_2PO_4^-}} = \frac{a_{H^+}}{K_2} \times f_1(pH) \tag{15}$$

and

$$f_3(pH) = \frac{(P_T)}{a_{PO_4^{---}}} = \frac{a_{H^+}}{K_3} \times \frac{(P_T)}{a_{HPO_4^{--}}} = \frac{a_{H^+}}{K_3} \times f_2(pH). \tag{16}$$

According to equation 11, the activity coefficient of each phosphate ion depends solely[4] on the ionic strength of the solution. Therefore, if the activity of hydrogen ions (or the pH) and the ionic strength are known, any of the functions $f_1(pH)$, $f_2(pH)$, or $f_3(pH)$ is completely determined.

Because of the many terms and operations involved, the calculation of activities of phosphate ions in solution is laborious. A simplification is effected by a tabulation of $f_1(pH)$, $f_2(pH)$, or $f_3(pH)$ for different values of pH and ionic strength. Figure 1 shows a plot of the logarithm of the function $f_2(pH)$ versus pH for several values of ionic strength. The values employed for the constants in equation 13 in preparing the graph were $K_1 = 7.59 \times 10^{-3}$, $K_2 = 6.31 \times 10^{-8}$, and $K_3 = 4.79 \times 10^{-13}$, as given by Lindsay and Moreno (1960) for 25°C. Use of Figure 1 eliminates the laborious computations indicated in equation 13.

[4] The parameters A and B in equation 11 are temperature-dependent. The numerical values given in connection with the equation are for 25°C. Values for other temperatures are given by Manov et al. (1943).

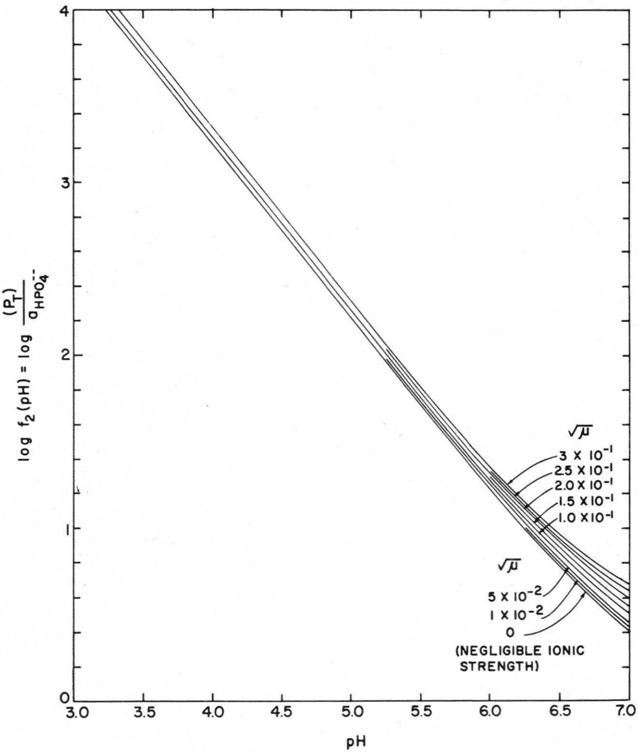

Figure 1. Plot of f_2(pH) against pH for different values of ionic strength.

The calculations are facilitated further by use of Table 1, which contains values of pH + log f_2(pH) calculated at different pH values and various ionic strengths. Because the plot of log f_2(pH) against pH is approximately that of a straight line with slope equal to -1 over a pH range of nearly three units for each ionic strength (Fig. 1), and because the lines representing the different ionic strengths are close together, Table 1 with entries equal to pH + log f_2(pH) is composed of numbers exhibiting only relatively small variations over that pH range. The table is thus especially suitable for interpolation over proper ranges of pH and of ionic strength. Subtraction of the corresponding pH value from any entry in the table gives the value of $\log f_2(\mathrm{pH}) = \log \dfrac{(P_T)}{a_{HPO_4^{--}}}$ for the particular ionic strength and pH value to which the entry corresponds. The activity of HPO_4^{--} ions can then be calculated readily by dividing the total molar phosphorus concentration by the value of f_2(pH). The activities of $H_2PO_4^-$ and PO_4^{---} are obtained from those of HPO_4^{--} and H^+ by means of equations 8 and 9.

Table 1. Values of pH + log f_2(pH) for different values of pH and of ionic strength.

pH	Values of pH + log f_2(pH) corresponding to indicated values of the square root of the ionic strength: 0	$1x10^{-2}$	$5x10^{-2}$	$1x10^{-1}$	$1.5x10^{-1}$	$2x10^{-1}$	$2.5x10^{-1}$	$3x10^{-1}$
3.25	7.23	7.24	7.25	7.27	7.29	7.30	7.32	7.33
3.50	7.22	7.22	7.24	7.26	7.28	7.30	7.31	7.32
3.75	7.21	7.21	7.23	7.25	7.27	7.29	7.30	7.32
4.00	7.20	7.21	7.23	7.25	7.27	7.28	7.30	7.31
4.25	7.20	7.21	7.23	7.25	7.26	7.28	7.30	7.31
4.50	7.20	7.21	7.23	7.25	7.26	7.28	7.30	7.31
4.75	7.20	7.21	7.23	7.25	7.26	7.28	7.30	7.31
5.00	7.20	7.21	7.23	7.25	7.27	7.28	7.30	7.31
5.25	7.20	7.21	7.23	7.25	7.27	7.29	7.30	7.32
5.50	7.21	7.22	7.23	7.26	7.27	7.29	7.31	7.32
5.75	7.21	7.22	7.23	7.26	7.29	7.30	7.32	7.34
6.00	7.22	7.23	7.25	7.28	7.30	7.32	7.34	7.36
6.25	7.24	7.25	7.28	7.30	7.33	7.36	7.38	7.40
6.50	7.27	7.29	7.31	7.35	7.38	7.41	7.44	7.46
6.75	7.33	7.34	7.38	7.42	7.45	7.49	7.52	7.55
7.00	7.41	7.42	7.46	7.51	7.56	7.60	7.64	7.68

It is customary to express activities in terms of their negative logarithms to the base 10 and to indicate this operation with the letter "p." Thus, operationally, p is defined by

$$p = -\log\,(\text{number}).$$

Performing this operation on equations 8 and 9 and, for the sake of simplicity, letting the symbol for each element or radical without parentheses stand for the activity, the following equivalent relations are obtained after rearranging:

$$pH_2PO_4 = pHPO_4 + pH - pK_2 \tag{17}$$

and

$$pPO_4 = pHPO_4 - pH + pK_3. \tag{18}$$

Similarly, from equations 12, 13, and 14, the following three relations are obtained in terms of negative logarithms:

$$pH_2PO_4 = p(P_T) + \log f_1(pH), \tag{19}$$

$$pHPO_4 = p(P_T) + \log f_2(pH), \tag{20}$$

and

$$pPO_4 = p(P_T) + \log f_3(pH). \tag{21}$$

The following example may be given to show the procedure for obtaining the activities of the various phosphate ions. For a solution with a pH value of 5.25 and ionic strength 6.25×10^{-2}, the square root of which is 2.5×10^{-1}, Table 1 gives the entry 7.30. Subtraction of the pH value from this figure yields $\log f_2(pH) = 2.05$. If the total phosphorus concentration, as determined experimentally, is equal to 1×10^{-5} ($p(P_T) = 5.00$), equation 20 yields $pHPO_4 = 5.00 + 2.05 = 7.05$. With the values $pK_1 = 2.12$, $pK_2 = 7.20$, and $pK_3 = 12.32$ given by Lindsay and Moreno (1960), equations 17 and 18 yield

$$pH_2PO_4 = 7.05 + 5.25 - 7.20 = 5.10$$

and

$$pPO_4 = 7.05 - 5.25 + 12.32 = 14.12.$$

The value of pH_2PO_4 can be obtained directly by subtracting 7.20 from the particular entry in Table 1 and then adding the result to the value of $p(P_T)$. In the above example,

$$pH_2PO_4 = 5.00 + (7.30 - 7.20) = 5.00 + 0.10 = 5.10,$$

as obtained before. This relation is a consequence of equation 15, which may be rewritten as

$$\log f_2(pH) = -pH + pK_2 + \log f_1(pH),$$

or

$$\log f_1(pH) = (\log f_2(pH) + pH) - pK_2, \tag{22}$$

which corresponds to

$$\log f_1(pH) = (\text{entry from Table 1}) - pK_2.$$

Substitution of the last equation in 19 yields the value of pH_2PO_4 directly in terms of the entries from Table 1.

Activities of Calcium and Other Ions

In studies of the solubility of phosphate rock, there is need for information on the activities of calcium, hydrogen, and fluoride ions in addition to the phosphate ions. Activities of hydrogen ions are measured directly. Activities of fluoride ions are not measured because of uncertainty of the degree to which the fluoride in solution is present in the form of a complex silicofluoride ion. As a substitute for this information, the solubility-product constant for calcium fluoride may be employed under certain circumstances, as indicated subsequently.

In the absence of sulfate, the activity of calcium may be derived from the product of the molar concentration of calcium, found by analysis, and the activity coefficient found from equation 11. According to Kielland (1937), the parameter $10^8 a_i$ in the equation has the value 6 for calcium.

In the presence of sulfate the problem is more complex because sulfate ions associate to some extent with both calcium and magnesium ions to form molecular sulfates of calcium and magnesium. Money and Davies (1932) give the dissociation constants of these two species as 0.0053 and 0.0063:

$$\frac{[\gamma_{Ca^{++}} \cdot (Ca^{++})]\ [\gamma_{SO_4^{--}} \cdot (SO_4^{--})]}{(CaSO_4)} = 0.0053 \tag{23}$$

and

$$\frac{[\gamma_{Mg^{++}} \cdot (Mg^{++})]\ [\gamma_{SO_4^{--}} \cdot (SO_4^{--})]}{(MgSO_4)} = 0.0063 \tag{24}$$

If the total concentration of calcium, magnesium, and sulfate found in solution by analysis are represented by x, y, and z, respectively, the concentration of the ions are evidently given by

$$(Ca^{++}) = x - (CaSO_4), \tag{25}$$

$$(Mg^{++}) = y - (MgSO_4), \tag{26}$$

and

$$(SO_4^{--}) = z - (CaSO_4) - (MgSO_4). \tag{27}$$

In the absence of magnesium, equations 24 and 26 may be disregarded, and equation 27 reduces to

$$(SO_4^{--}) = z - (CaSO_4). \tag{28}$$

Substituting 25 and 28 in 23 and solving for $(CaSO_4)$,

$$(CaSO_4) = \tfrac{1}{2}\left[x + z + \frac{0.0053}{\gamma_{Ca^{++}} \cdot \gamma_{SO_4^{--}}}\right]$$

$$\pm 1/2\left[\left\{x + z + \frac{0.0053}{\gamma_{Ca^{++}} \cdot \gamma_{SO_4^{--}}}\right\}^2 - 4xy\right]^{1/2} \tag{29}$$

Observed values for x and z and trial values for $\gamma_{Ca}{}^{++}$ and $\gamma_{SO_4}{}^{--}$ then are substituted into equation 29. The trial values for $\gamma_{Ca}{}^{++}$ and $\gamma_{SO_4}{}^{--}$ are obtained from equation 11 using x and z as trial values for the ionic concentrations of calcium and sulfate, respectively, and using Kielland's (1937) values of $10^8 a_i = 6$ for Ca^{++} and 4 for SO_4^{--}. Equation 29 then may be solved to obtain a trial value for $(CaSO_4)$. This value is substituted in equations 25 and 28 to obtain improved estimates of (Ca^{++}) and (SO_4^{--}); these in turn are used in 11 to obtain improved estimates of $\gamma_{Ca}{}^{++}$ and $\gamma_{SO_4}{}^{--}$, and the latter are entered in equation 29 to obtain an improved estimate of $(CaSO_4)$. This new estimate of $(CaSO_4)$ then is substituted in equations 25 and 28 to obtain new values for (Ca^{++}) and (SO_4^{--}), and the process is continued in the manner just described until the values for (Ca^{++}) and (SO_4^{--}) and the respective activity coefficients do not change appreciably. As a check on calculations, the numerical values employed in the last approximation may be substituted in equation 23 to see whether the indicated equality is satisfied.

In the presence of magnesium, the activity of calcium may be calculated approximately by assuming that the behavior of calcium and magnesium is identical with regard to formation of an undissociated sulfate. This approximation is a relatively good one (and is probably sufficient for the purpose at hand) because the dissociation constant of calcium sulfate is only slightly less than that of magnesium sulfate, because the activity coefficient of calcium is slightly greater than that of magnesium at the same ionic strength, and because these differences are partially compensating. The procedure is to enter the sum of the total molar concentrations of calcium and magnesium as x in equation 29 in the preceding paragraph and to follow the directions given there to obtain an apparent value of (Ca^{++}). This value is partitioned into (Ca^{++}) and (Mg^{++}) in the same proportion as the total concentrations of the respective elements. The value of (Ca^{++}) thus obtained is multiplied by the value obtained from equation 11 for $\gamma_{Ca^{++}}$ in the final approximation.

A more accurate value for $a_{Ca^{++}}$ in the presence of sulfate and magnesium may be obtained with the aid of equations 30 and 31. Equation 30 is derived from equations 23 through 27. The term (Ca^{++}) is eliminated between 23 and 25; (Mg^{++}) is eliminated between 24 and 26; $(MgSO_4)$ is eliminated between 27 and the equation resulting from combination of 24 and 26. Finally (SO_4^{--}) is eliminated between the equation resulting from combination of 23 and 25 and the equation resulting from combination of 24, 26, and 27, giving

$$\frac{0.0106\ (CaSO_4)}{[\gamma_{Ca^{++}} \cdot \gamma_{SO_4^{--}}][x - (CaSO_4)]} - z + y + (CaSO_4) + \frac{0.0063}{\gamma_{Mg^{++}} \cdot \gamma_{SO_4^{--}}}$$

$$\pm \sqrt{[z - y - (CaSO_4) - \frac{0.0063}{\gamma_{Mg^{++}} \cdot \gamma_{SO_4^{--}}}]^2 + [\frac{0.0252}{\gamma_{Mg^{++}} \cdot \gamma_{SO_4^{--}}}][z - (CaSO_4)]}$$

$$= f(CaSO_4) = 0 \tag{30}$$

Equation 30 may be solved for $(CaSO_4)$ in the following manner. As a first approximation, the value of $(CaSO_4)$ obtained from the procedure of the preceding paragraph is substituted into equation 30, along with values of x, y, and z, and along with values of $\gamma_{Ca^{++}}$, $\gamma_{Mg^{++}}$, and $\gamma_{SO_4^{--}}$ that can be calculated, once the approximate value of $(CaSO_4)$ has been found. To calculate $\gamma_{Mg^{++}}$, Kielland's (1937) value $10^8 a_i = 8$ is used in equation 11. The resulting expression for $f(CaSO_4)$ is then evaluated, and the numerical values obtained are plotted graphically against the guessed value of $(CaSO_4)$. A new guessed value of $(CaSO_4)$ then is employed, and the function is evaluated again. The numerical values of $f(CaSO_4)$ again are plotted against the guessed value of $(CaSO_4)$. The process is repeated until, by interpolation, it is possible to find the guessed value of $(CaSO_4)$ required to reduce $f(CaSO_4)$ to 0. The value of $(CaSO_4)$ thus obtained is substituted into equation 31, which is solved for $(MgSO_4)$. Equation 31 is obtained by dividing 23 by 24, substituting 25 and 26 in the result, and rearranging.

$$(MgSO_4) = \frac{0.84y \cdot \gamma_{Mg^{++}}}{\frac{x \cdot \gamma_{Ca^{++}}}{(CaSO_4)} - \gamma_{Ca^{++}} + 0.84\gamma_{Mg^{++}}} \tag{31}$$

These approximate values for ($CaSO_4$) and ($MgSO_4$) are substituted in equations 25, 26, and 27 to obtain new values for (Ca^{++}), (Mg^{++}), and (SO_4^{--}), which in turn are employed in 11 to obtain new values of $\gamma_{Ca^{++}}$, $\gamma_{Mg^{++}}$ and $\gamma_{SO_4^{--}}$. With these new values for $\gamma_{Ca^{++}}$, $\gamma_{Mg^{++}}$ and $\gamma_{SO_4^{--}}$ entered in equation 30, the value of ($CaSO_4$) required to reduce f($CaSO_4$) to 0 is found, the result is substituted in equation 31 for ($MgSO_4$), and so on, until the numerical values do not change appreciably in successive approximations. As a final check on the computations, the results may be substituted in equations 23 and 24 to determine whether the indicated equalities are satisfied. The value of $a_{Ca^{++}}$ then may be calculated from the values of $\gamma_{Ca^{++}}$ and (Ca^{++}) employed in the last approximation.

In addition to the associations with sulfate, both calcium and magnesium associate with hydroxyl. Robinson and Stokes (1955, p. 400) give dissociation constants of $MgOH^+$ and $CaOH^+$ as 0.0026 and 0.05, respectively. These constants are large enough that the effects may be neglected for the purpose of estimating activity coefficients and ionic concentrations of calcium and magnesium except perhaps in strongly alkaline solutions.

Diagrammatic Representation of Solubility Relations of Calcium Phosphates

Each sparingly soluble crystalline calcium phosphate is characterized by a unique solubility-product constant at a particular temperature. This constant is the product of the activities of the ions furnished by the compound to an aqueous solution in equilibrium with the compound, each activity being raised to the power represented by the subscript indicating the number of the particular ionic units in a single molecule of the solid compound. For example, octocalcium phosphate has the formula $Ca_4H(PO_4)_3 \cdot 3H_2O$. The expression for the solubility-product constant is

$$a^4_{Ca^{++}} \cdot a_{H^+} \cdot a^3_{PO_4^{---}} = \text{solubility product constant.}$$

In the conventional negative-logarithmic form, this expression becomes

$$4pCa + pH + 3pPO_4 = \text{p solubility-product constant,}$$

where the symbol p represents the negative logarithm, and the symbols for the ions represent the activities of the ions.

Conformance of the activity-product with the solubility-product constant for a particular calcium phosphate species in an experimental situation such as analyses of an aqueous extract of soil is evidence that the solution is in equilibrium with that species in the soil. For the purpose of comparing different calcium phosphates and examining the transitional conditions frequently encountered in practice, however, solubility-product constants are not particularly useful. Eriksson (1952), Aslyng (1954), and others have adopted a more suitable way of representing the results, namely, a two-dimensional plot of $(pH_2PO_4 + \frac{1}{2}p(Ca)$ against $(pH - \frac{1}{2}pCa)$. A plot of values of $(pH_2PO_4 + \frac{1}{2}pCa)$ against those of $(pH - \frac{1}{2}pCa)$ for solutions in equilibrium with a particular crystalline calcium phosphate at a particular temperature should produce a straight line that is characteristic of the phosphate species in question. Each other calcium phosphate having a solubility-product constant should have a separate and characteristic straight line. Lines for the various phosphates may be represented in a single two-dimensional diagram, which facilitates comparison of different phosphates and representation of intermediate conditions. Because of the utility of the procedure, some comments on its significance may be warranted.

The activities of ions in aqueous solutions in equilibrium with a particular calcium phosphate obey in general a relation of the form,

$$ApH + BpCa + CpH_2PO_4 = D, \tag{32}$$

where A, B, C, and D are constants for each crystalline calcium phosphate species, and where $(C/2) - (A/2) = B$. Accordingly, equation 32 may be rewritten as

$$A(pH + \tfrac{1}{2}pCa) + C(\tfrac{1}{2}pCa + pH_2PO_4) = D. \tag{33}$$

Equation 32 represents a plane in a coordinate system with three orthogonal axes, namely, the pH axis, the pCa axis, and the pH_2PO_4 axis. Any set of data, pH, pCa, and pH_2PO_4, that satisfies equation 32 with parameters appropriate for a particular phosphate will produce a point on the solubility plane for that phosphate. Equation 33 is a transformation of 32 representing a line in a coordinate system with two orthogonal axes, namely, $(pH + \frac{1}{2}pCa)$ and $(\frac{1}{2}pCa + pH_2PO_4)$.

In this transformation, any point in the three-dimensional space is mapped as a point in two-dimensional space; all the points in any particular plane in the three-dimensional space are mapped as points on a particular straight line in the two-dimensional space; and all the points that lie along straight lines oriented in a particular way on the plane in the three-dimensional space are mapped as individual points in the two-dimensional space, one point corresponding to each line. Plots of $(\frac{1}{2}pCa + pH_2PO_4)$ against $(pH + \frac{1}{2}pCa)$ for various calcium phosphates are shown in Figure 2.

Solubility of Hydroxyapatite

Hydroxyapatite is a sparingly soluble compound with the composition $Ca_{10}(OH)_2(PO_4)_6$. If an aqueous solution of hydroxyapatite exists in a state of equilibrium with the solid material, conformity with the solubility-product principle requires that, in the solution,

$$a^{10}{}_{Ca^{++}} \cdot a^2{}_{OH^-} \cdot a^6{}_{PO_4{}^{---}} = \text{constant}. \tag{34}$$

If the activities of the ions are represented in the conventional negative-logarithmic form, equation 34 may be written

$$10pCa + 2pOH + 6pPO_4 = 113.7 \tag{35}$$

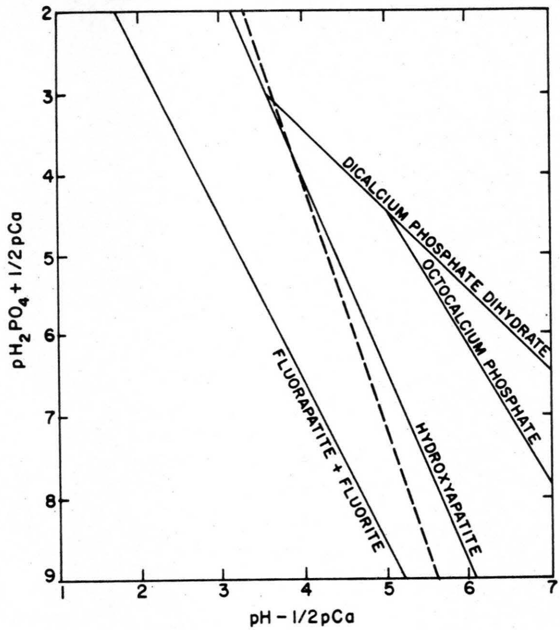

Figure 2. Plot of ($pH_2PO_4 + \frac{1}{2}pCa$) against ($pH - \frac{1}{2}pCa$) for solutions in equilibrium with different calcium phosphates. The broken line represents an alternative formulation for hydroxyapatite proposed by Rootare *et al.*, as explained in the text.

where, for simplicity, the symbol of the ion represents the activity, and where 113.7 is the value given by Lindsay and Moreno (1960) for the negative logarithm of the constant in equation 34.

Equation 35 may be transformed to the form of equation 33 in the following manner. The term $a_{HPO_4^{--}}$ is eliminated between equations 8 and 9. The resulting equation is solved for $a_{PO_4^{---}}$ and expressed in negative logarithmic form to yield

$$pPO_4 = pK_2 + pK_3 + pH_2PO_4 - 2pH. \quad (36)$$

Introducing the expression,

$$pOH = pK_w - pH = 14 - pH, \quad (37)$$

for the ionization constant of water, and substituting 36 and 37 in 35, one obtains, after rearranging the terms and substituting the appropriate numerical values for pK_2 and pK_3, the equation,

$$7pH - 5pCa - 3pH_2PO_4 = 15.71. \quad (38)$$

The term $-5pCa$ may be represented as $-3/2\ pCa - 7/2\ pCa$, as mentioned in connection with equation 32; hence, equation 38 may be rewritten as

$$7(\mathrm{pH} - \tfrac{1}{2}\mathrm{pCa}) - 3(\tfrac{1}{2}\mathrm{pCa} + \mathrm{pH_2PO_4}) = 15.71. \qquad (39)$$

Equation 39 is shown as one of the lines in Figure 2.

Experimental work with the calcium phosphates has disclosed some complexities relative to the solubility behavior. Procedures described in the literature for preparation of hydroxyapatite involve heating the precipitate in water, usually at 100°C at atmospheric pressure, but sometimes at several hundred degrees and relatively high pressures. Products obtained at 100°C or lower temperatures are finely divided crystals; those obtained at higher temperatures may consist of crystals up to 0.3 mm in length (Perloff and Posner, 1960). At ordinary temperatures, however, one or more calcium phosphates less basic than hydroxyapatite are almost certain to be present (dibasic calcium phosphate is a common product) and usually are the major constituents in the original precipitates. These substances may persist indefinitely; or, if the soluble products of hydrolysis are removed, the phosphate remaining in the solid residue gradually changes to hydroxyapatite (Schleede, Schmidt and Kindt, 1932). The more soluble substances will dominate the solubility behavior and may exert an effect even where they are present in quantities too small to permit their detection by X-ray diffraction. With careful attention to preparation of materials, however, several investigators have obtained values of a solubility-product constant for hydroxyapatite that are in fairly good agreement.

If the dissolution of hydroxyapatite is a process involving true solubility, the ionic constituents should appear in solution in the same ratio as they occur in the solid, and the concentration of ionic constituents in solution should be unaffected by the ratio of solution to solid as long as undissolved solid remains. Rootare, Deitz, and Carpenter (1962) found, however, that the concentration of the solution decreased with increasing ratio of water to solid and that the ion-activity-product for hydroxyapatite decreased steadily with an increase in the proportion of the solid dissolved. The ratio of calcium to phosphorus in the solution increased steadily with the proportion of the solid dissolved and approached the theoretical value of 5Ca to 3P where 15 to 20% of the material had dissolved. To account for the observations the authors postulated that the solubility phenomena do not represent the true solubility of hydroxyapatite but rather the solubility of a surface complex formed upon hydrolysis of the terminal phosphate ions in the hydroxyapatite crystals according to the following reaction:

$$\mathrm{Ca_{10}(OH)_2(PO_4)_6} + 6\mathrm{H_2O} = 4\mathrm{Ca_2(OH)_2HPO_4} + 2\mathrm{Ca^{++}} + 2\mathrm{HPO_4^{--}}. \qquad (40)$$

The surface complex then dissolves according to the equation,

$$\mathrm{Ca_2(OH)_2HPO_4} = 2\mathrm{Ca^{++}} + 2\mathrm{OH^-} + \mathrm{HPO_4^{--}}. \qquad (41)$$

Although both reactions supply calcium and phosphate ions to the solution, the ions in solution tend toward an equilibrium with the surface complex. According to this postulate, the ion-activity-product for hydroxyapatite is not the proper one to formulate to represent the equilibrium; rather, the ion-activity-product should be

$$2pCa + 2pOH + pHPO_4 = 27.3, \tag{42}$$

which is derived from reaction 41. The value 27.3 is the average result Rootare et al. obtained from their own investigations and from recalculated data of others. While equation 42 may not be a true thermodynamic solubility expression, it was found by Rootare et al. to be more nearly applicable than the ion-activity-product calculated on the basis of the composition of hydroxyapatite. The improved constancy of the ion-activity-product is noticeable even after the difference in magnitude of ion-activity-products for hydroxyapatite and the proposed surface complex is taken into account.

Equation 42 may now be modified to permit representation of the postulated equilibrium in the two-dimensional solubility diagram described in the preceding section. According to quation 8,

$$a_{HPO_4^{--}} = \frac{a_{H_2PO_4^-} \cdot K_2}{a_{H^+}},$$

which may be rewritten as

$$pHPO_4 = pH_2PO_4 + pK_2 - pH.$$

Substituting this expression in 42 yields

$$2pCa + 2pOH + pH_2PO_4 + pK_2 - pH = 27.3.$$

Noting that $pOH = 14 - pH$ and that $pK_2 = 7.20$,

$$2pCa + 28 - 2pH + pH_2PO_4 + 7.20 - pH = 27.3,$$

which may be rearranged to

$$3(pH - \tfrac{1}{2}pCa) - (\tfrac{1}{2}pCa + pH_2PO_4) = 7.9. \tag{43}$$

Equation 43 is plotted in Figure 2, along with the solubility line derived from the "theoretical" solubility-product constant for hydroxyapatite. The two lines may be seen to be similarly located and actually to cross, so that values of $(\frac{1}{2}pCa + pH_2PO_4)$ and $(pH - \frac{1}{2}pCa)$ for certain solutions would be close to either line.

Solubility of Fluorapatite

Fluorapatite is a sparingly soluble compound with the composition $Ca_{10}F_2(PO_4)_6$. According to the solubility-product principle, a saturated solution of fluorapatite will satisfy the relation,

$$a^{10}_{Ca^{++}} \cdot a^2_{F^-} \cdot a^6_{PO_4^{---}} = \text{constant}. \tag{44}$$

In negative logarithmic form,

$$10pCa + 2pF + 6pPO_4 = 118.4, \tag{45}$$

where the value of the constant is taken from Lindsay and Moreno (1960).

To transform equation 45 to the form of equation 33, use is made of the equation for the solubility-product constant of calcium fluoride, which is

$$pCa + 2pF = 9.84 \tag{46}$$

The value of the constant is that given by Lindsay and Moreno (1960). If equation 46 is substituted in 45, the term 2pF may be eliminated. If equation 36 is substituted in the resulting equation, pPO_4 may be replaced with an expression containing pH_2PO_4. Noting that (C/2) - (A/2) = B, as mentioned in connection with equation 32, one may rearrange the final equation and reduce it to the form,

$$6(pH - \tfrac{1}{2}pCa) - 3(\tfrac{1}{2}pCa + pH_2PO_4) = 4.28. \tag{47}$$

Equation 47 is plotted as one of the lines in Figure 2. Because of use of the expression for the solubility-product constant of calcium fluoride to eliminate the term 2pF, the final equation is a representation of the solubility of fluorapatite in a saturated solution of calcium fluoride. Whether fluorapatite hydrolyzes or reacts with fluoride to form a surface complex, as proposed by Rootare, Deitz, and Carpenter (1962) for hydroxyapatite, has not been investigated.

Solubility of Hydroxyfluorapatite

According to Beevers and McIntyre (1946), the atomic structure of apatite is made up of calcium, oxygen, and phosphorus atoms arranged in a network traversed by channels containing negative ions that balance the excess positive charge of the basic lattice. Hydroxyl and fluoride are both monovalent negative ions and are of similar size, and the lattice charges may be balanced by either ion species or by a mixture of the two.

If the charge unbalance of the calcium-oxygen-phosphorus network is satisfied by a uniform mixture of fluoride and hydroxyl ions, the specimen in question is said to be a solid solution of fluorapatite and hydroxyapatite (hydroxyfluorapatite). In an aqueous solution in equilibrium with such a specimen, the activities of the ion species in solution should satisfy the ion-product expressions for both fluorapatite and hydroxyapatite, each multiplied by a factor that depends on the molar fraction of that constituent in the solid phase. Thus, where the molar fraction of fluorapatite is N and that of hydroxyapatite is (1 - N), the ion-product expressions may be represented as

$$a^{10}_{Ca^{++}} \cdot a^{6}_{PO_4^{---}} \cdot a^{2}_{F^-} = K' = K_{FA} \cdot F'(N) \tag{48}$$

and

$$a^{10}_{Ca^{++}} \cdot a^{6}_{PO_4^{---}} \cdot a^{2}_{OH^-} = K'' = K_{HA} \cdot F''(1 - N), \tag{49}$$

where K_{FA} and K_{HA} are the solubility-product constants for fluorapatite and hydroxyapatite, K' and K'' are constants for each particular value of

N, and F' and F'' indicate functional relations. The functional relations must satisfy the requirement that $F'(N) = 1$ where $N = 1$ and that $F''(1 - N) = 1$ where $(1 - N) = 1$. Equations 48 and 49 may be written in negative-logarithmic form like equations 35 and 45, and the resulting equations may be transformed further to the form of equations 39 and 47. Accordingly, if ($\frac{1}{2}$pCa + pH_2PO_4) is plotted against (pH - $\frac{1}{2}$pCa), the straight line appropriate for fluorapatite may be expected if N = 1 (see Fig. 2). With a series of solid solutions having successively lower values of N, one would expect a series of straight lines, oriented in the same general direction as the fluorapatite and hydroxyapatite lines, and proceeding from the fluorapatite line where N = 1 to the hydroxyapatite line where N = 0. Alternatively, if the solubility relations of hydroxyapatite are properly represented by the surface-complex concept of Rootare, Deitz, and Carpenter (1962), discussed in the preceding section, equation 49 should be replaced by

$$a^2_{Ca^{++}} \cdot a_{HPO_4^{--}} \cdot a^2_{OH^-} = K'' = K_{\text{surface complex}} \cdot F''(1 - N), \tag{50}$$

and the plots of ($\frac{1}{2}$pCa + pH_2PO_4) against (pH - $\frac{1}{2}$pCa) for solid solutions of hydroxyfluorapatite should lie intermediate between those for fluorapatite and the surface complex. At least in a general way, therefore, some inferences about the relative values of N for different specimens may be made from the comparative locations of the lines in the plot of ($\frac{1}{2}$pCa + pH_2PO_4) against (pH - $\frac{1}{2}$pCa).

The foregoing comments relative to the formation of straight lines in a plot of ($\frac{1}{2}$pCa + pH_2PO_4) against (pH - $\frac{1}{2}$pCa) apply to the condition in which a given value of N applies to the entire line. As will be reported subsequently, the lines obtained where relatively large quantities of acid are added to separate samples of a hydroxyfluorapatite may not be straight because of a change in value of N from a secondary reaction following dissolution. Nevertheless, the lines appear to be straight under less extreme conditions; and one then has some confidence in inferences based on assumed constancy of N.

These considerations are pertinent to a theoretical investigation of the solubility behavior of phosphate rocks in which the principal and most soluble phosphatic constituent is a hydroxyfluorapatite. Because under acid conditions the solubility of hydroxyapatite exceeds that of fluorapatite, one would expect that the higher is the molar fraction of hydroxyapatite in a solid solution of fluorapatite and hydroxyapatite (the lower is the value of N), the greater should be the equilibrium concentration of phosphorus in aqueous solutions in contact with it. The greater solubility should result in greater availability of the phosphorus to plants.

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[1] A circulating copy of each complete thesis is available in the Iowa State University Library, Ames, Iowa. Abstracts of these theses are published in Dissertation Abstracts, A microfilm or a photostat copy of a thesis may be purchased from Dissertation Microfilms, 313 N. 1st Ave., Ann Arbor, Michigan.

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Editor

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