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Volume XIII

Number 5

BOTANICAL PAPERS. II

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IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

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NOTES ON IOWA FUNGI, 1929-30

G. W. MARTIN

1. *Gnomonia veneta* on white oak

Gnomonia veneta (Sacc. and Speg.) Kleb. is an extremely common parasite on sycamore and has long been known to attack several species of *Quercus*. In Gilman and Archer's list of the parasitic fungi of Iowa¹ it is reported as occurring on both *Q. alba* and *Q. macrocarpa*. It is, however, rarely conspicuous and seems as a rule to do little harm to these hosts. In May 1930, following a month of cool, moist weather, it was abundant and serious on *Quercus alba* in Iowa City. It was especially severe on trees growing in sheltered situations, such as ravines, while trees growing in more exposed situations had only the leaves on the lower branches affected. Great differences were noted in the susceptibility of different individual trees to the disease, certain trees being severely attacked, others, standing beside them and exposed to the same environmental conditions being almost untouched. This difference was especially conspicuous among seedlings. Red oak was unaffected.

The Gloeosporium stage of the fungus was fruiting abundantly on the diseased leaves while they were still on the tree.

2. *Sebacina atrata* Burt

Sebacina atrata as originally described by Burt² was based on material collected by Dr. Farlow in Massachusetts. Apparently the only other known collection was by the same distinguished mycologist in New Hampshire. In October, 1930, it was found growing on the bark of a large fallen oak at Homestead, Iowa County. When fresh, the fructification was watery gray and extremely soft, forming a thin and somewhat reticulate layer on the bark, looking like a myxomycete plasmodium, which at first it was taken to be. It dries into a very

¹Iowa State Coll. Jour. Sci. 3:350. 1929.

²Ann. Mo. Bot. Gard. 2:765. 1916.

thin blackish film. Our material agrees in all respects with Burt's description. The spores (fig. 1) are rather broad for this genus and in our specimen measure 9-10 x 5.5-6 μ .

3. *Sebacina calospora* Bourd. and Galz.

Sebacina calospora seems not to have been heretofore reported from America. Our material consists of a minute patch, a few millimeters in extent, growing on oak. The curious flexuous fusiform, sometimes branched spores, 20-30 μ in length (figs. 2, 3) are like nothing else except the similar spores of *Tulasnella calospora* (Boud.) Juel, reported by Burt³ from Maine. The two may indeed be varying manifestations of the same species. The Iowa material, collected at Iowa City in November, shows basidia of typical tremellaceous type, with cruciate-septate hypobasidia and cylindrical epibasidia, as in *Tremella* (fig. 4). Side by side with these may be found basidia with thick epibasidia almost as in *Tulasnella*, and basidia with sterigmata borne almost directly on the hypobasidial segments (fig. 5). Several cases were observed where a single epibasidium bore two sterigmata (fig. 6). In all cases, however, the mature hypobasidia were septate to the base. The basidia of this species, suggesting, as they do, the basidia of certain species of *Tulasnella*, form an additional argument for the close relationship of that genus with the Tremellaceae.

4. The genus *Tulasnella* in Iowa

The genus *Tulasnella* was established by J. Schroeter in 1888⁴. As early as 1872 the brothers Tulasne⁵ had illustrated a *Tulasnella* under the name *Corticium incarnatum* Fr. and had suggested its relationship with the Tremellaceae, hence it is appropriate that Schroeter should have named it as he did. About two months after Schroeter's paper appeared, Patouillard published independently his genus *Prototremella*⁶ and the following year Johan-Olsen published *Pachysterigma*⁷.

The species of *Tulasnella* are resupinate fungi with the aspect of *Peniophora* or of the thin waxy species of *Sebacina*.

³Ann. Mo. Bot. Gard. 13:328. 1926.

⁴Pilze Schles. 1:397. June 2, 1888.

⁵Ann. Sci. Nat. (bot.) 5 ser. 15:234, Pl. 10, f. 3-5.

⁶Jour. de Botanique 2:267. 1888.

⁷in Brefeld, Untersuch. 8:5. 1889.

The basidia, however, are unlike those of any other genus. At first subglobose or pyriform, as in *Tremella*, they do not become septate, but develop at the tips usually four swollen, sessile, spore-like bodies. Into these the protoplasm from the original pyriform structure passes, after which the latter usually collapses, and each of the secondary bodies develops a sterigma and a spore. Much confusion has existed as to the nature of these various structures, and varying interpretations have resulted in taxonomic confusion.

Schroeter listed *Tulasnella* as an Anhang to the Tremellaceae. Brefeld, because the basidia are unseptate, put the genus in his group *Autobasidiomycetes*, in the *Tomentellaceae*, just below *Hypochnus*. In this he has been followed by authors of numerous works on fungi, of whom it will suffice to mention Burt⁸ and Gäumann and Dodge⁹. Other systematists have taken a different view. Juel¹⁰ established the family *Tulasnellaceae* for these forms. In this he was followed by Patouillard¹¹ and by many modern European students, including Rea¹² and Bourdot and Galzin¹³. Killermann¹⁴ discards the family *Tulasnellaceae* and includes *Tulasnella* in the Tremellaceae.

In my judgment the *Tulasnellaceae* are sufficiently distinct from the Tremellaceae to justify regarding them as a separate, but closely allied family. The classification of Patouillard (l.c.) is clarified by the discussion and terminology of Neuhoff¹⁵, which permits correlation of the basidia of the two groups at all stages. The pear-shaped or subglobose probasidia are entirely similar. In the Tremellaceae, in typical examples, the probasidia become longitudinally cruciate-septate, and each of the four segments so formed sends out a cylindrical and usually tortuous epibasidium. In the *Tulasnellaceae* the old basidial cavity is completely drained of its protoplasm by

⁸Ann. Mo. Bot. Gard. 6:253-259. 1919; id. 13:328. 1926.

⁹Comp. morph. of fungi, p. 431. 1928.

¹⁰Bihang Svenska Vet. Ak. Handl. 23, III, No. 12:21. 1897.

¹¹Essai taxonomique, p. 26. 1900.

¹²British Basidiomycetae, p. 739. 1922.

¹³Hymen. de France 1:54. 1927.

¹⁴Die nat. Pflanzenf. 2 ed. 6:114. 1928.

¹⁵Bot. Archiv 8:262. 1924.

the formation of the four oval or fusiform epibasidia, which are finally cut off by septa. The effect in both cases is the same; to divide all the protoplasm into four portions, each portion to be used, with its nucleus, for the formation of a basidiospore. The cylindrical epibasidia of the Tremellaceae and the oval epibasidia of the Tulasnellaceae, and it may be added, the slender epibasidia of the Auriculariineae and the stout forked arms of the Daeromycetinae, are commonly called sterigmata, but in all of the cases mentioned, the true sterigmata are perfectly apparent at the tips of these structures, and are in size, shape and function much like the sterigmata of an agaric, as Buller¹⁶ has shown.

Juel (l.c.) studied two species of Tulasnella, for which he erroneously established his new genus Muciporus. He believed that the globose spore-like bodies were true spores, germinating in place. Juel's figures and observations do not, however, necessarily lead to this conclusion but may better be interpreted in accordance with the views of Patouillard and Neuhoff.

In recent years, a number of species have been recorded, mostly from Europe. Bourdot and Galzin list eighteen species of Tulasnella and four of Gloeotulasnella. Few collections have been reported from North America. Burt (l.c.) lists four species: *T. Eichleriana*, *T. violea*, *T. fusco-violacea*, and *T. calospora*. Two localities cited are in Canada, the others are either east of the Alleghenies or west of the continental divide. Overholts¹⁷ reports *T. violea* from Pennsylvania. There are apparently no reports from the Mississippi Valley. It is of interest therefore, to record the finding in Iowa of three of the four species listed by Burt.

T. Eichleriana Bres. is distinctive because of its very small spores. It was first found on an old oak branch at Iowa City, growing not on the wood, but overrunning an old rotten fructification of a Pyrenomycete with its delicate lilac arachnoid growth. We have two later collections on similar substrata. The spores are subglobose or broadly oval 4-6, rarely 7 μ x 3-4 μ (fig. 7). The epibasidia are at first globose, then fusi-

form, when mature 6-9 x 3.5-4 μ . These figures agree very closely with those given by Burt and by Bourdot and Galzin (figs. 9, 10).

T. violea (Quel.) B. and G. is very close to the preceding species. It is a little more robust in every way—texture firmer, thicker and with larger hyphae, basidia, epibasidia, and spores. The spores are broadly oval, 6-7 x 3.5-4.5 μ (fig. 11), the epibasidia oval, then fusiform 8-10 x 3.5-6 μ (figs. 12, 13). Homestead, Iowa County.

T. fuscoviolacea Bres. is the largest and most brightly colored of the three. We have several collections, all from near Iowa City, on both frondose and coniferous wood, always very old and rotten and decayed by other fungi, leading to a suspicion that it is saprophytic upon the remains of the other fungi rather than on the wood. When fresh, it is pallid lilaceous, close to pale purple drab of Ridgway, waxy, thin, easily separable from the substratum as a white membranous tissue. It dries pale pinkish, light vinaceous fawn of Ridgway. The aspect of the fungus is that of a thin pallid Peniophora. It is easily overlooked, and this, together with the fact that it seems to occur only in the late fall, winter and early spring, may explain why it has not been collected more frequently.

Bourdot and Galzin describe the spores as oblong, obliquely narrowed at base and laterally depressed, 7-12 x 4.5-6 μ . Burt says "elongated," 10-15 x 3.5 μ . His illustration shows them as somewhat allantoid or fusiform. A spore print is easily secured. The spores are pale lilac in mass, hyaline under the microscope, pip-shaped, 7-10 x 4-6 μ (fig. 17), agreeing essentially with Bourdot and Galzin's measurements. The epibasidia are oval, elongated, then irregularly fusiform, 9-14 x 4-8 μ (figs. 15, 16, 18). In all of the species studied the epibasidia are easily detached after they are cut off by a septum from the hypobasidium, but that is particularly the case with the present species. Under such circumstances they may readily be taken for spores (fig. 18). Careful examination will show, however, that every such epibasidium is provided with a sterigma or a sterigmatic base but not an apiculus, while each spore has an apiculus, but not a sterigma unless it is preparing to germinate by producing a secondary spore, in which case the sterigma is always at the tip of a longer or

¹⁶Researches on fungi. Vol. 2:156 ff. 1922.

¹⁷Bull. Torrey Bot. Cl. 49:166. 1922.

EXPLANATION OF PLATE I

Figure 2 drawn at a magnification of 1110 diameters using camera lucida, and reduced in reproduction to 683 diameters. All other figures drawn at a magnification of 2436 diameters and reduced to 1500 diameters.

Fig. 1. *Sebacina atrata* Burt. Two spores showing large oil drop.

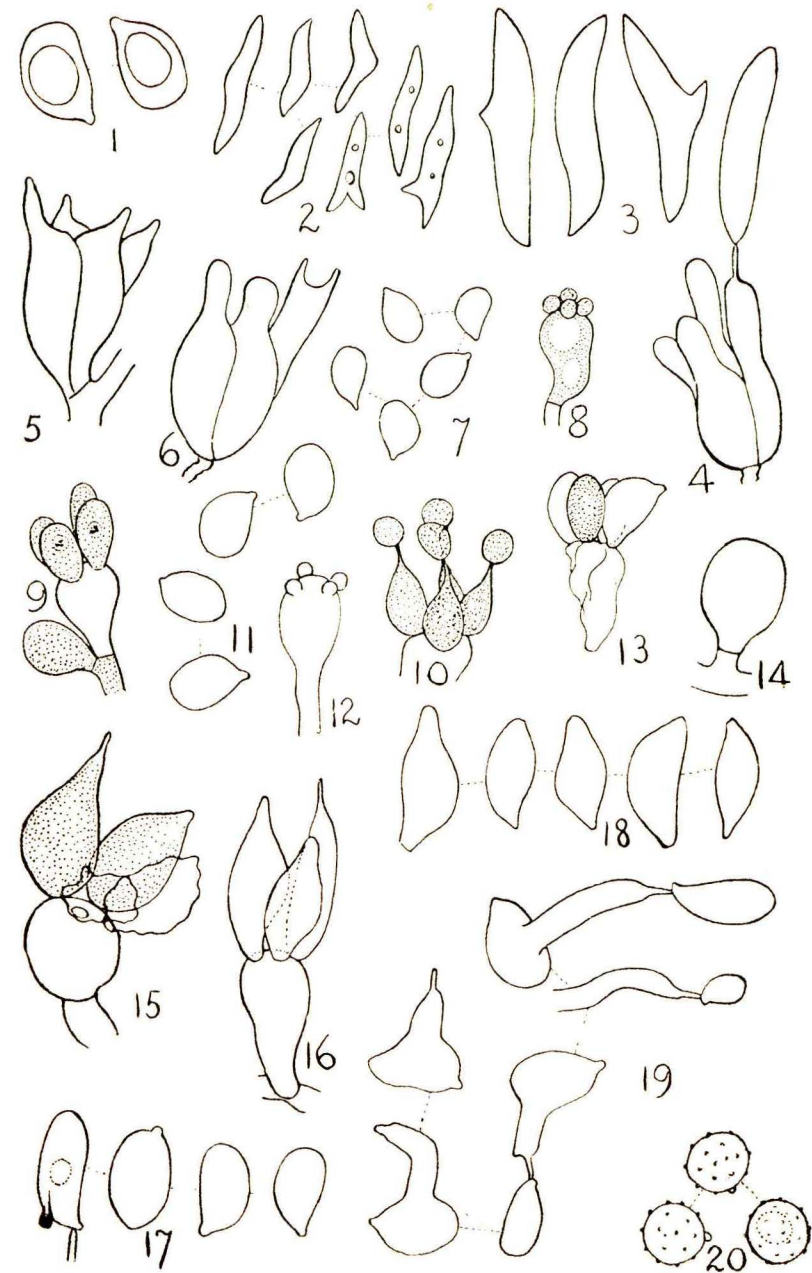
Figs. 2-6. *Sebacina calospora* Bourd. and Galz. 2. Seven spores, to show variation, x 683. 3. Three spores. 4. Normal basidium, with one spore still attached. 5, 6. Abnormal types of basidia.

Figs. 7-10. *Tulasnella Eichleriana* Bres. 7. Spores from a spore print. 8. Basidium with epibasidia just developing. 9. Hypobasidium emptied of protoplasm; epibasidia full size and cut off, but sterigmata not yet formed; below, a probasidium. 10. Formation of basidiospores on epibasidia.

Figs. 11-13. *Tulasnella violea* (Quél.) B. and G. 11. Spores from a spore print. 12. Young basidium. 13. Old basidium; one epibasidium has not yet borne a spore, the other three have discharged their spores but have not yet collapsed; the hypobasidium has collapsed.

Figs. 14-19. *Tulasnella fuscoviolacea* Bres. 14. Probasidium, showing lateral attachment to mycelium often seen. 15. Basidium; hypobasidium empty but not collapsed, two epibasidia have discharged their spores and collapsed, the other two have not yet formed their spores. 16. Basidium with three epibasidia. 17. Four basidiospores to show variation in size and shape. 18. Five spore-like detached epibasidia. 19. Germination of basidiospores; four shown, two with secondary spores still attached, also tip of an extra long germ tube growing from a basidiospore sunk within the gelatinous surface of the hymenium.

Fig. 20. *Corticium effuscatum* Cooke and Ellis. Three spores.



shorter germ tube and nearly always lateral (fig. 19). It seems certain that Burt has confused spores with epibasidia or so-called "sterigmata" that have become detached.

5. *Corticium effusatum* Cooke and Ellis

A common and widespread species, but apparently not heretofore reported from Iowa. It is easily recognized in the field by its bright salmon fructifications. An abundant collection was made in the Amana Colony woods in Iowa County in October, 1930. The spores are pale salmon in mass, and in mounts made from a spore print I cannot distinguish any difference between chlamydospores and basidiospores. Both are hyaline, globose or nearly so,—not even, as stated by Burt¹⁸ but covered with sparse but distinct tubercles (fig. 20).

6. *Coniophora cerebella* Persoon

This is an important wood destroying fungus common throughout Europe and the northern part of North America. It is recorded from Iowa by Burt but we have had no collections in the University of Iowa herbarium. In the fall of 1930 it was abundant in the vicinity of Iowa City, occurring on fallen apple, ash, and oak branches and on oak and white cedar fence posts.

7. *Coniophora arida* (Fr.) Karsten

A widespread and important wood-rotting species, at first sight suggesting *C. cerebella*, but dry, not fleshy, and with a nearly smooth or pulverulent-tuberculate surface. On cedar fence post, Iowa City, November, 1930. Not previously represented in our collections.

STUDIES IN IOWA PLANT-LIFE. I. THE GENERA EQUISETUM, QUERCUS, AMELANCHIER AND FRAXINUS IN THE OKOBOJI FLORA

ARTHUR PIERSON KELLEY

The flora about the Okoboji Lakes in northwestern Iowa constitutes one of the best remaining portions of original prairie. Here there is not a narrow strip of wayside grassland with rich interweaving of aestival blossoms but broad acres of virgin prairie upon an undulating glaciated upland, with lakes and hydrarch succession in the moraine, with stream and wooded flood plains and oak bluffs adjacent. Accepting the concept of Pound and Clements (7) that the whole of the American western grassland area should be called prairie province, regardless of the degree of aridity, and the contention of Gleason (5) that the term "prairie" should be applied only to these American grasslands, and not to meadows, as Continental ecologists use the term, we have in the region of the Okoboji Lakes one of the most favorable areas for study of prairie.

According to Pound and Clements (l.c.), our area is contained in their Region I, the prairies proper; but an examination of the flora shows an admixture of species from Region III, the Foothill Region (of the Rockies). Such a condition becomes intelligible upon study of a climate-map (6) upon which the mean annual precipitation is indicated as being less in the northwestern corner of the state of Iowa than in the remainder of the state. Consequently, we are not surprised to find cacti and tar-weed growing here in addition to a more mesic flora.

The Iowa Lakeside Laboratory being situated in the midst of this region so exceptionally favorable for study, the students have engaged in detailed consideration of certain groups of plants which, possibly through a greater plasticity, appear to differ from those forms with which they have been customarily placed.

¹⁸Ann. Mo. Bot. Gard. 13:248. 1926.

1. Equisetum: Besides the ubiquitous *E. arvense* L., two other Equiseta grow in the area. These were studied critically by Mr. D. George Deihl, of the State University of Iowa, who concluded that the two species are *E. kansanum* Schaffner and *E. hyemale* L. A careful study of stem-portions removed from the herbarium sheets, softened and sectioned, brought us to the conclusion that those plants formerly referred to *E. laevigatum* A. Br. and *E. variegatum* var. *Jesupi* A. A. Eaton are apparently all *E. kansanum*. One area of our plants, on the Floete Prairie, was identified as this species by Dr. Schaffner himself, when he visited our region. The varieties *robustum* (A. Br.) A. A. Eaton and *intermedium* A. A. Eaton of *E. hyemale* L. depend upon characters which can be found on different stems of a single clump of plants, and these varieties are consequently included for the present with the species.

2. Quercus: The common oak of northwestern Iowa is the bur oak, *Q. Michauxii* Muhl. The white oak, *Q. alba* L., has been recorded(8) from the area, but the writer was unable to find any of this species, and Mr. John B. Eisen, of Grinnell College, was also unable to locate any white oak in our area.

Much of the bur oak forest about the Okobojis is an even age stand of sprout origin, the timber having been clean-cut about fifty-five years ago. The forest is composed of trees averaging nine inches diameter at breast height and fifty feet height. In the primaeval forest, many of the bur oaks were 100 to 150 feet high and four to five feet in diameter(4), but it is doubtful if any trees of this size ever grew in the Okoboji region. Annual increment in bur oak is rather small, being 0.25 to 0.33 inches according to Van Horn(9) and in the vicinity of Grinnell (central Iowa), 0.30 inches, according to Conard(3). Reproduction studies revealed the unlooked-for fact that bur oak is not reproducing in Elm Crest, along the Little Sioux and in Emmet County. In Elm Crest, seedlings would seem to average normally less than 100 per acre while the present stand is approximately 700 trees per acre. Neither is the present stand maintaining itself: there are about 80 trees dead per acre while a considerable fraction of the stand has partially dead crowns. Reproduction is predominantly of ash (*Fraxinus campestris*) with locally equal elm (*Ulmus fulva*). Whatever may have been the succession in the

past, the present succession would seem to be from bur oak to ash-elm forest. Our conclusion thus rather coincides with that of Woodward(12) who considered the oaks as pioneers. We are probably to consider, however, the true pioneers to be *Rhus glabra* and *Symphoricarpus orbiculatus* and *S. occidentalis* (1), which species are then followed by oak.

Some of the bur oaks are said by Dr. Shimek to approach the dwarf form known as var. *depressa* (Nutt.) Engel., and he states that: "The form is clearly an ecological variety which grades into the type, but it is convenient to retain the name for ecological discussions." (l.c., p. 39.)

In addition to bur oak, a red oak is commonly found in the Okoboji region. Fruiting branches of our trees, sent to an eastern herbarium for authoritative determination, were returned with the information that they were in part *Quercus rubra*, in part *Q. ellipsoidalis*; but the collector had neglected to state that branches of both sorts had been collected from a single tree. This incident illustrates the fact that there is decided variability in size and shape of both acorn and cupule, but we have not as yet made the fruits the subject of special study. The tree itself makes better growth than bur oak, being 10-11 inches diameter at breast height and 65-70 feet high at about forty years of age, while its reproduction appears sufficient to maintain the stand. Red oak is apparently a cosere with ash-elm forest.

Bode(2) distinguishes between Red Oak (*Quercus borealis* Michx. f. = *Q. rubra* L.; l.c., p. 37) and Black Oak (*Q. ellipsoidalis* E. J. Hill) as components of the Iowa native tree-flora. It has been realized since the time that Sargent published his notes in Rhodora (15:39, 1915; 18:45-48, 1916) that *Quercus rubra* L. is in reality the tree which has been known as *Q. falcata* Michx.: while the northern red oak, formerly called *Q. rubra* L., is *Q. borealis* Michx. f. and its variety *maxima* (Marshall) Ashe, a tree which ranges from the Appalachian region westward to eastern Nebraska and central Kansas. *Q. ellipsoidalis*, described by E. J. Hill in the Botanical Gazette (27, 1899), has been considered as ranging from Indiana into eastern Iowa.

3. Amelanchier: The Amelanchiers of the Okoboji region are shrubs of varying habit, which in days past have been called in part *A. canadensis* (L.) Medic., in part *A. spicata* (Lam.)

Koch. The last is not *A. spicata* K. Koch, which is considered a hybrid of *A. oblongifolia* x *stolonifera*?, but the species of C. Koch. This species, according to the Britton and Brown Illustrated Flora is found "In dry rocky places, Ontario to Michigan, Iowa, Pennsylvania, and North Carolina." In Peepoon's Flora of the Chicago Area (p. 342, 1927), it is stated: "No one of late seems to find this plant. It is characteristically northern." The species is made synonymous with *A. canadensis rotundifolia* Michx., although in the 7th edition Gray's Manual, the *Mespilus canadensis* var. *rotundifolia* Michx. is called a synonym of *A. spicata* Robinson and Fernald. Wiegand (10), in his monographic study, states that the Robinson and Fernald species is synonymous with *A. sanguinea* (Pursh) D. C., while the species of C. Koch is kept distinct from any of the species in the monograph. The Kew Index lists the species as "*A. spicata*, C. Koch Dendrol. i 182 = *canadensis*?". *A. canadensis* (L.) Medic. ranges (according to Wiegand, l.c.) "from Washington Co., Maine, and from western New Hampshire to Iowa, Kansas and Missouri, and southward to Georgia and Louisiana."

The Okoboji specimens seemed so different to those with which the writer was familiar in the Atlantic States, that he was glad when Mr. Claude Pampel, Principal of the Flanagan, Illinois, High School, made an examination of such material as was available in July and August, 1930, in the region.

Ours are more or less stoloniferous shrubs of 1-5 m. height, the most being from 2-3 m. high. The rather sparse and somewhat repent branches bear essentially glabrous leaves of 35-55 mm. length (a few attaining to 85 mm.) and 40-45 mm. breadth; with petiole length from 12-24 mm., the majority being from 18-21 mm.: In shape, then, the leaves are rounded to round-ovate. The apex is usually distinctly pointed but sometimes it is rounded or even sub-truncate, while the base is rounded or sub-truncate. The margin is coarsely toothed, the serrations extending back from the apex two-thirds of the way to the petiolar insertion, and there are 3-4 teeth per cm. The teeth are characteristically crenate-dentate, with a mucronate point somewhat proximal of the center. The uppermost veins run straight into the teeth, but more

distally the veins branch dichotomously once or twice before reaching the tooth, and thus one major vein is made to serve two or more teeth. Fruiting specimens were not available, but data on the fruit were kindly supplied by Mr. B. O. Wolden in a letter to the writer, from which he takes the liberty of quoting: "I believe when you were here at Estherville you took specimens from a round-leaved form which I consider to be *sanguinea*, and of another which has larger flowers than usual. The round-leaved form, of which I do not seem to have a flowering specimen, has lower pedicels in fruit about 15 mm. long and shallow hypanthium. Length of petals I do not know, but think they are average large or about 10 mm. long. The other, with more pointed leaves, has petals 12 mm. long; lower pedicels (in flower) 10 mm. long, in fruit up to 16 mm.; hypanthium 4 mm. in diam., and about 2 mm. deep. As far as I have ever seen, all our forms have the top of ovary hairy. Through numerous forms the size of the flowers grades down to a very small-flowered form which is common at Estherville, with petals about 6 mm. long, lower flowering pedicel barely 5 mm. long; or, on more mature specimens, 8 mm. (no fruiting specimen), with hypanthium narrow (3 mm.) and deep (2 mm.)."

The characters so far given differ from those assigned to *A. sanguinea* in:

The Okoboji Amelanchier	<i>A. sanguinea</i>
1. Some of plants stoloniferous	Not stoloniferous
2. Height, av. 2-3 m.; max. 5 m.	Height 1-2.5 m.
3. Leaves commonly orbicular, 40-45 mm. broad	Leaves rarely orbicular, 25-40 mm. broad
4. Margin never or rarely toothed to base	Margin toothed to near base
5. 3-4 teeth per cm.	4-5 (6) teeth per cm.
6. Uppermost veins spreading	Uppermost veins strongly ascending
7. Hypanthium 3-4 mm. dia.	Hypanthium 5 mm. dia.

From *A. grandiflora* Wiegand, a separate from *A. sanguinea*, our plants differ in the shorter pedicels (not over 15 mm.,

others short-stalked. The leaflets are lanceolate to ovate, and serrate to serrulate. The samara has a terete body with the wing decurrent to the middle, the wing slightly notched, blunt, or mucronulate.

The original description of the Prairie ash, *Fraxinus campestris* Britton, which appeared in North American Trees (p. 799-800; fig. 726, 1908), is as follows: "This tree, which ranges from Montana to Manitoba, Wyoming and Kansas, preferably inhabiting valleys, has been confused with the eastern Red ash (*Fraxinus pennsylvanica* Marshall), from which it differs in its shorter-stalked or sessile lateral leaflets which are relatively broader, and in its shorter fruit.

Its bark is thick, brown and rough. The young twigs are round and either smooth or velvety. The leaves have 7 leaflets for the most part, which are ovate to ovate-lanceolate, usually long-pointed and toothed and more or less hairy beneath, rarely smooth on both surfaces. The flowers are dioecious with a small 4-toothed calyx. The samaras are spatulate, averaging about 3 cm. long, the blunt or little notched wing decurrent upon the narrowly conic seed-bearing part to its middle or below.

The wood is similar to that of the Red ash, and is used for similar purposes. The type specimen was collected by Rev. J. M. Bates at Long Pine, Nebraska, August 9, 1897."

While the writer has not seen the type specimen, he has seen authoritatively determined specimens; and he has collected the species in Red Willow Co., Nebraska, and in Pennington Co., South Dakota. In the Plains region, the species has a short and often gnarled stem, and the leaves are comparatively small, coriaceous, with decided points to the leaflets, and in all cases a rather close hairiness upon them. On the other hand, the eastern Red ash often has almost sessile leaflets; and in examining the large collection of specimens of "*Fraxinus pennsylvanica* Marsh" at the United States National Museum we are impressed with the amount of variation in leaf and samara character. Regarding source of material in correlation with structure, just as in *Amelanchier*, we note that those from moist regions are thin-leaved and more or less smooth, while those from more arid regions are xeromorphic in having smaller leaves and hairiness, regardless

of petiole character. The ash of the Okoboji region is not fitted exactly by the description of either Red or Prairie ash, but is intermediate in character, just as are other specimens of the north central region of the Mississippi Valley. To separate the Okoboji material in varietal or form-rank would necessitate a simultaneous separation of others which would in all cases be founded on indefinite characters; and it seems wiser to the writer to include the Okoboji ash with its nearest congener, the Prairie ash.

In addition to the foregoing observations, we may note that plants called *Oenothera biennis* are not necessarily *Oe. biennis* L.; as a matter of fact, most of them are probably not that species, but until a more critical study of the group is made (as, we understand, is being made in Professor Conard's Department at Grinnell College), we cannot do better than aggregate our evening primroses together under one name.

January, 1931.

Malvern, Pennsylvania.

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THE WATER SUPPLYING CAPACITY OF PRAIRIE SOIL, AS INDICATED BY OBSERVATIONS ON A VIRGIN PRAIRIE IN NORTHWESTERN IOWA

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The volume of water in soil is of no necessary concern to the student of vegetation. The plant is affected by available water of the usually three-phase system, and this water is supplied to the plant at a certain rate. Water supplying capacity of the soil may be inferred from studies made with use of the porous clay cones, familiarly known as "soil-points," which were invented by Livingston and Koketsu (9). The porous surfaces are of a definite area, delimited by shellaced surfaces. The soil-point is inserted in the soil, allowed to remain there for one hour, after which it is removed to a screw-cap vial, taken to the laboratory and weighed. Increase in weight is considered due to liquid taken in from the soil.

Significance of the term "prairie"

The prairies offer a particularly favorable site for study. The word "prairie," originally meant to designate a meadow, has come to mean a province or area in which may be found plant communities ranging from marsh to aquatic on the one hand, or, through meadow and prairie, to forest or steppe on the other. The prairie is essentially a grass-land community which is exposed to xeric influences; its mostly geophytic or hemicryptophytic plants form a dense sod, not a bunched plant community as in the steppe: Distinction between prairie and "dry prairie" or steppe has not always been carefully made.

Water loss from prairie soil

The plant covering of the prairie, being sociable to the fifth degree, makes a considerable demand upon the environment: Roots of prairie plants extend from five to seven feet beneath the surface (13). Then, too, there is almost constant

evaporation from the surface-soil as long as water is present therein, for the prairie soil is exposed to a considerable insolation, and wind velocity. It is not exposed to full insolation, for the plant covering interposes somewhat of a screen; and wind velocity varies with topography. The water lost from the prairie soil must be replaced if plants rooted in it are to live; moreover the roots are placed at different levels in the soil. While Rotmistrov, among others, discussed the distribution of soil moisture within the soil profile, we have had no information hitherto upon the water supplying capacity of soil at different depths.

The region studied

Observations were made in the summer of 1930 on virgin prairie soil of northwestern Iowa, on the southwest quarter of section 23, township 99 north, range 37 west, Dickinson County. True virgin prairie probably exists no longer but the area studied approaches virgin condition in that it has never been plowed and seldom grazed, although for several years it was mowed to provide prairie-hay. Studies were also made on prairie sod of the nearby campus of Iowa Lakeside Laboratory. The soil is morainic, partially altered by physical erosion and to a considerable extent has contained boulders which have been broken down by chemical weathering. The soil profile ordinarily exhibits beneath a small amount of graminaceous duff about 20-40 cm. of black soil humus, usually merging with a brownish sandy loam at less than a half-meter depth. The *B* horizon is of great thickness.

Methods

In study of the water supplying capacity of these soils (in reality the absorbing capacity of porous cones is observed), the soil-points were inserted into soil, which in the case of the first observations was loosened, after which loose soil was packed about the point, for with the exception of places where the soil had been moistened through some cause, it was baked into adobe-hardness by the heat of the exceptional summer of 1930. Water supplying capacity of the soil at different depths was studied by removing blocks of soil with a trenching spade, and at once inserting the soil points at 25 cm. and (in other excavations) at 50 cm. depth. The

following day the 25 cm. hole was excavated to 50 cm. depth and used as indicating conditions at that depth, since first trials indicated no difference of reading whether the old excavation was used or a new one made. The holes were kept covered by reinserting the plug of sod upon top of the hole. The first observations were made between the hours of 4 and 5 in the afternoon, but most of the work was done before 8 in the morning. At the end of one hour after insertion the soil-points were transferred from soil to screw-cap vials and were at once taken to the laboratory and weighed.

For the soil-study, three stations were established, one on a hilltop (steppe plant community), a second on a slope (true prairie), and a third in a shallow draw or slough (prairie-meadow transition). That which was called true prairie supported a *Poa-Stipa-Koeleria* community while the transitional area indicated moister conditions through such plants as *Lilium Michiganense* Farwell and *Lacinaria pycnostachya* (Michx.) Ktze.

The vegetation

On the steppe there is naturally a community of widely spaced and deeply rooted plants, but even among these the species which depend for water supply upon secondary roots, as *Solidago nemoralis* Ait., had numerous dead members. In the prairie, many plants which were more shallowly rooted (as e.g., *Verbena stricta* Vent.) died and a "dry prairie" community was formed by selection of the most deeply rooted sorts.

The establishment of plants on the prairie depends (*inter alia*) upon their ability to subsist within the soil profile. For perennial species this means, in addition, through a period of years, for some years are exceptionally dry or wet. Usually the earlier summer is comparatively rainy and many seedlings germinate and become rooted, only to be killed by late summer drought. The ease with which weed species, as *Ambrosia*, become rooted in grazed prairie sod; the abundance of such native plants as *Oxalis* in tough mats of *Poa* on the prairie; the not infrequent successful invasion of forest trees into prairie sod, make any hypothesis for explaining the treeless condition of prairie based on inability of trees to make entrance into the sod seem questionable. The ideas which have

been advanced from time to time by Dr. Shimek (12) regarding the treelessness of the prairies are undoubtedly correct: the prairie flora is xeric. Trees differ from those herbaceous plants which send a primary root or a series of secondary roots into the sub-soil where they may secure moisture; forest tree roots, with their mycorrhizal root-endings, linger in the humus region of the top-soil, and are consequently killed when summer drought sets in. *Quercus macrocarpa* was observed by the writer to quickly develop a tap root and to produce even the first year a considerable mycorrhizal system at some depth, thus apparently differing somewhat from other species. This oak is able to survive a continued drought and under favorable conditions of a succession of moist vegetative seasons may invade to some distance in the prairie sod from the parent plants, which, with the rest of the prairie-province forest vegetation, are confined to the borders of streams and lakes where a greater supply of soil-moisture is available. Bur oak, however, does not reproduce freely in the forest, since the acorns germinate on the litter, project the radicle into the duff in a moist season, and the plantlets are then dried up and killed in a succeeding dry season. Only where the soil is exposed can the seedling quickly send its roots into a moist substratum and thus survive.

It is noteworthy that Clements, Weaver and Hanson (3) found in their transplant studies of competition that seedlings of *Gleditsia triacanthus* (*sic*: *G. triacanthos* L.?), *Acer negundo*, *Acer saccharum*, *Tilia americana*, *Ulmus americana* (? : *U. americana*) is sparse in the prairie region in comparison to *U. fulva* Michx.), and *Fraxinus lanceolata* (? : *F. campestris* Britton?) from seeding and transplants died out within three years on the prairie, except in case of the *Gleditsia* of which 60% survived and in *Acer negundo* of which 50% survived. *Fraxinus* made the poorest record, which is attributed to "the more or less vertical growth of the main roots and the almost complete absence of a superficial portion so pronounced in the honey-locust, maple and box-elder." But on examination of the data presented by the authors, we find that of the 76 experimental plants of all species studied, the following died:

3 "of drought"

36 "the first season" or "in year"

21 "died in first summer" or "in summer"

11 "winter-killed" or "in winter"

The five plants which survived were of species which do not have the mycorrhizal relation established to the same complexity as in *Acer saccharinum*, *Tilia americana*, and *Ulmus (fulva?)*; *U. americana* has the same habit), all of which have "necklace" endotrophic rootlets while *Gleditsia triacanthos* and *Acer negundo* have simple mycorrhizae and roots of plastic habit which, in drier soil, penetrate deeply (even as figs. 11-12, i.e., indicate for *Gleditsia triacanthos*). Fraxinus, having expansive thinner leaves and probably a considerable transpiration stream, makes a greater demand on the environment for water and is less able to survive on the prairie.¹ The five individuals out of the 76, with deeper root-penetration, through physiological resistance to wilting, or to peculiarly favorable conditions of their particular habitat, survived while the others died. This experiment gives a clear picture of the normal life-process of tree species invading the prairie.

Precipitation and water-absorbing power of the air

During the period of study there was almost no precipitation. There was no rain from July 3 to August 9, and no rain of consequence until August 19. No records are available but the precipitation in all was probably not 2 mm. depth before August 19.

Atmometer stations were established for observation of the evaporating capacity of the air, one being placed on the campus on a table one meter high, the other on the virgin prairie at 3 dm., i.e., at level of vegetative organs of larger prairie plants. The two stations were not strictly comparable, since one was on the prairie (protected from the prevailing west wind by a slight swell of the prairie, it is true) while the other was on the campus, somewhat within the "kettle" of a lake and more or less protected by some buildings and trees. The corrected readings are appended as for 24 hour periods since division into hourly periods would give meaningless figures; there is probably almost momentary fluctuation in evaporation from the machine, although there is a

¹Ash comes into the prairie only as a successor to oak.

grand period of evaporation rate. It was interesting to observe that almost no evaporation occurred from the black spheres upon dark or cloudy nights, but on clear nights as the moon waxed there was a progressive increment in the evaporation rate, indicating that the atmometer spheres could be used profitably in studies of e.g. nyctotropic movements of leguminous leaflets.

RECORD OF ATMOMETER READINGS

Aug.	Laboratory Station		Floete Prairie	
	White sphere	Black sphere	White sphere	Black sphere
	S 29-493	S 29-564	S 29-518	S 30-69
2	71	96	70	106
3	71	86	48	85
4	61	72	48	71
5	48	67	44	66
6	29	44	30	50
7	32	47	36	52
8	38	48	33	54
9	39	48	35	52
10	27	39	30	40
11	35	47	35	50
12	38	46	40	55
13	40	53	41	57
14	19	31	20	33
15	42	58	35	54
16	45	59	36	55
17	25	32	32	49
18	26	32	36	46
19	15	19	16	22
20	5	10	4	9

Water-supplying capacity of surface- and sub-soil

Daily observations from August 2-8 indicated that the steppe soil could not supply water to the soil-points either at the surface or in sub-soil to 0.5 m. depth. In the other soils, the soil-points observed in a 1-hour period with little variation, from August 2-8:

	Prairie	Prairie-transition
Surface	0 mg.	0-5 mg.
25 cm.	10 mg.	20 mg.
50 cm.	20 mg.	40 mg.

With a greater number of tests and with balances more sensitive than the torsion balances used, significant variation in the results might have been noted.

By digging into the subsoil of the prairie, it was found that at a depth of a meter there was perceptible moisture while at a meter and a half the soil could supply moisture at the rate of incipient drying in the Maryland loam described by Wilson(14). No comparison of undisturbed sod with a denuded area was made, similar to that described by Baldwin (1).

A brisk shower upon the surface on August 9 enabled prairie soil to cause an increase in weight of the soil-points of from 120-230 mg. The rainfall did not penetrate into the subsoil but evaporated back into the air. A considerable rainfall on August 19 caused the soil-points to increase in weight by 4500 mg. in an hour when they were inserted in the surface; five hours later the soil-points took up only 500 mg. in an hour, while the moisture had not penetrated beyond 4 cm. depth. We may note in this connection a remark which Dr. Cameron(2) includes in a footnote in his book: "Dr. George N. Coffey drew the author's attention to some observations in western Kansas, where a prolonged drought had dried the soil to a considerable depth. A fairly heavy rain wetted the soil to less than two feet from the surface, and practically all of this moisture had returned to the surface and evaporated within a few days"(l.c. p. 23).

Israelsen and West(5) concluded that moisture applied to the surface moves down until it reaches the water table, but it must be noted that these authors dealt with a soil which had been *flooded*. In order to have downward movement there must be sufficient water applied to the surface to not only satisfy the physical demands of the soil's water holding capacity for that particular soil, but to provide the field capacity, whereupon particles may be detached by gravity to percolate downwards, or, in the case of flooding, free water slips downward through the inter-particle spaces past the capillary films of the soil particles through action of gravity alone.

A slight rainfall, accordingly, penetrated the soil at a slow rate. The black soil humus is of course rich in colloid and during the exceeding dryness of the summer the soil even on hill-tops had shrunk and cracked, somewhat as mud cracks in an exposed lake bottom. In order to gain an idea how

fast water moves through the soil, a stream of water was allowed to run from a hose upon prairie sod for an hour; the soil was then allowed to drain for another hour before soil-points were inserted. It was found that on a 7 degree slope, after insertion for an hour, the soil-points had increased in weight:

At end of hose	1040 mg.
0.5 m. downhill from hose	450 mg.
1.5 m. downhill from hose	15 mg.

With depth, it was found that in soil of another similar spot, the soil-points had increased in weight:

Surface	3451 mg.
35 cm. depth	1040 mg.
50 cm. depth	770 mg.

This hole was excavated to something over a meter depth, into gravel, without appearance of dry soil.

It was further noted that 10,000 cc. of water poured from a bucket into dry soil which supplied no moisture to porous cones, into a hole of approximately 10 liter capacity, disappeared (as free water) into the soil in 19.5 minutes. The moisture moved to an indeterminate depth in the vertical direction, but to only 7 cm. in the horizontal. Lateral movement was not uniform but was retarded by lenses of denser material.

Slow capillary movement of moisture in prairie soil is indicated, therefore, by:

- (1) Complete dryness of A horizon in absence of precipitation
- (2) Small lateral movement of water supplied to dry soil

Prairie soil is retentive of moisture where the soil is properly mulched. Two old hay-stacks rest on the area; beneath 3 dm. of naturally packed hay, after six weeks of drought, the soil yielded no moisture to the soil-points, but underneath 6 dm. of compacted prairie hay the inserted soil-points increased in weight by 1730 mg. in an hour.

Observations on a colloid-poor soil

These observations are exactly in accord with earlier ones made by the writer on Sassafras sands of the New Jersey

pine barrens. A method for estimation of "suction force" described for soils had been detailed by Joffe and McLean(6), by which a porous clay cup was inserted into the soil, filled with water, attached to a mercury manometer; and the height of the risen mercury column was considered indicative of the "suction force" of that soil. The first criticism of this method was by Hardy(4) who stated that the method "takes no account of variations in water conductivity of soils." Using Gram and Ampt's method of capillary coefficients for measurement of the "suction force," this writer concluded that it was not sufficiently precise as to be practical, "although less open to criticism on theoretical grounds than Joffe and McLean's method." Subsequently, the present writer(7) pointed out that no "suction force" was indicated either in field or laboratory beyond a certain point when *Sassafras* sands of the Spotswood, New Jersey, pine barrens were used. Whether the apparatus was set up in dune sand or in swamp soil ("meadow" of the geological survey) there was a certain rise of the mercury column, after which there was no further action. In the laboratory the same was found true of soil the surface of which was sealed with a paraffin coating.

The writer's observations are well explained in the words of Shaw(11): "The 'suction' forces of soils, and indirectly the colloid content, can not be measured by the use of porous burned clay or porcelain cups, bulbs, or tubes, because these porous materials themselves have a high water lifting or 'suction' force. The soil may serve to remove the moisture from the surface of the material and thus make possible a continuation of the process until the weight of the mercury lifted overcomes the tensile strength of the water column or the forces which hold the water in the pores of the 'cup' material. The soil, however, would not carry any of the 'suction' force. It would function essentially the same as though it were lifting water from a free surface and would develop a water content essentially the same as that of the capillary rise."

The movement of water in soil

The *agents* which induce movement of water in soil are the particulate forces of gravity, capillary and thermal energy. Gravity brings water to deeper lying roots, but its general

effect is to remove water from reach of the plant, although at the same time it induces in the root a geotropic response that aids in bringing the root to water. Capillarity and thermal energy together keep the root supplied with moisture when moisture is an available subject for their activity.

The *sorts* of soil-water movement are: (1) *Percolation*: After rain or through any other cause whereby free water is brought into the capillary spaces of the soil (as by action of gravity on capillary soil films which have attained to field capacity) there is a downward movement of water, under the influence of gravity, between the capillary soil films, checked by friction with these films and, where the films are more tenuous, by capillary action. The effect of percolation on the plant, in so far as it restores the capillary soil films to an optimum for water-intake by the plant is beneficial, but during the process of such restoration the water of percolation is perhaps injurious through its lessening of the oxygen-supplying capacity of the soil atmosphere. (2) *Diffusion*: Diffusion can act only very slowly and through minute distances when the water is contained in the gel coatings of the soil particles. Such movement in its totality is probably of minor consequence to the plant. (3) *Movement under thermal influence*: By passage of moisture particles from the capillary soil film into the soil atmosphere under influence of increased temperature, diffusion through the free capillary spaces of the soil, and condensation upon the cooler soil particles, there is perhaps a considerable transport of liquid in the soil. Such provision for the plant is notably supplemented by probably the chief movement of water through the soil. (4) *Movement through capillarity*: Capillary movement of moisture in the soil depends upon a lessened capillarity within some region or upon some particles in the soil, for no movement could occur when the capillary films are in a state of equilibrium. This equilibrium may be upset by any agent which extracts water from the soil; the agent most active in upsetting the equilibrium is the evaporating power of the air. Upon passage of moisture particles from the soil surface into the air, the equilibrium between the capillary forces of the uppermost soil particles and those subjacent to them is upset, and moisture moves upward into the film on the uppermost particles from the

lower through capillarity and against gravity. This movement is propagated downward, and a movement of a considerable mass of water results.

The process as related to an osmometer study is described by Pulling and Livingston(10): "With the very inception of water absorption (i.e., by an osmometer), then, the attraction for water exhibited by the thin layer of soil next to the membrane is more or less markedly increased. Before this occurrence, however, our hypothetical system was supposed to be in static equilibrium, as far as water movement is concerned, and now we find that the slightly dried soil layer is attracting water more strongly than the more distant portions of the soil mass. After such a disturbance equilibrium must tend to recur, which must imply water movement from the more distant films to those which have been thinned. Thus the drying process is extended outward from the absorbing surface, and our process of absorption has now come to involve not only movement from soil to osmometer, but also movement from soil film to soil film. The latter phenomenon and its dynamics are apparently of fundamental importance to an appreciation of the water relation between plant and soil."

The movement of water within the plant and in the soil adjacent to the plant-body are induced by the same agent, but in the plant we have the added phenomena of a continuous column of liquid and negative pressure. It must be noted in passing, however, that the apparatus used by Dixon and subsequent workers does not duplicate the water-conducting structure of the plant. The Askenasy experiment involves the use of a continuous capillary tube of relatively thick and impermeable (glass) wall while the vessels of the plant are discontinuous, and the relatively thin and elastic vessel-walls are comparatively permeable, resulting in continuity in the radial as well as the longitudinal direction.

The distance to which water may be caused to move through soil by some such hypothetical action as we have supposed, is a question. It is well known that the surface films when excessively thinned may break, especially at the thin places in the lenses of capillary water. With such breakage and with continued insolation, capillary movement would cease, and

there would be drying of the soil nearest the evaporating agent.

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Malvern, Pennsylvania.

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