PLANT SUCCESSION ALONG MILL CREEK

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Although this investigation¹ included a study of (1) the early plant succession on the islands, (2) the plant succession on the creek bank, (3) the plant succession in the embryonic ravines, and (4) the effect of the various farm practices on these successions and on erosion, only the part dealing with the early plant succession on the islands and the plant succession on the creek bank is here considered. The area studied was limited to the mile of bank on the Knapp Farm near Nashville, Tennessee, and to the islands found in the creek here. The data were collected on weekly field trips during the autumn of 1923 and the summer and autumn of 1924 by the junior author.²

I. PLANT SUCCESSION ON THE ISLANDS IN MILL CREEK

At the point studied, Mill Creek has a bed of almost horizontal strata of limestone with two sets of joint planes running almost at right angles to each other. There are shallow pools and rapids.

Collections of stones may slow down the stream and cause deposition of gravel or sand on their leaward side. In such places, pioneer plants such as *Dianthera americana* L.³ may come in. Frequently, also this plant appears in the crevices of the joint planes that run transverse to the creek, either from seeds or fragments of the plant which lodge here, or by runners from plants on shore. Once started the plant spreads rapidly by underwater rhizomes which root at each joint.

This plant by its upright shoots slows down the stream so that it may drop part of its load. This gives additional foothold for the Willow Herb so that it becomes more abundant, thus further slowing down the stream and causing additional deposition. Through a continuance of this cycle, islands may be built up to the low water level as a direct result of the presence of the plant. At this stage the islands will be covered with a pure stand of *Dianthera americana* L. Stages in this process were studied immediately below the railroad bridge as well as at several other places farther down stream.

Bars of sand, gravel, or shingle may originate without the agency of plants, for anything that slows down a stream will cause deposition of a part of its load.⁴ In all cases American Willow Herb is the pioneer plant and aids markedly in the later deposition. The aerial shoots, rootstocks, and roots further check the stream's velocity and cause more suspended material to be deposited, thus increasing deposition and further increasing the area for plant invasion.

As the island or bar, through increased deposition, appears above the low water stage, Spike Rush (*Eleocharis* sp.) appears among the Willow Herbs. This Spike Rush is a leafless plant with tufted culms which grow nine to twelve inches high and produce terminal spikes in the early summer. The numerous upright shoots, fibrous roots, and matted rootstocks assist in island formation by causing deposition.

Apparently the Spike Rush can not grow under water or at least not as well as the Willow Herb, but it does require a very damp soil. When the Willow Herb is growing out of water, it becomes low, less vigorous, and seemingly more attacked by Dodder (Cuscuta obtusiflora HBK.) Under these conditions it is rapidly replaced by the Spike Rush so that the island appears with a center of Spike Rush and an outer zone of Willow Herb. With the Spike Rush (Eleocharis sp.) are likely to be a few other plants in anticipation of the next stage of succession. One such island, located below the middle pier of the railroad bridge, had the following plants scattered among the Spike Rush:

Rice Cut-grass (Leersia oryzoides [L.] Sw.)
Frank's Sedge (Cyperus Frankii Kunth.)
Lancaster's Sedge (Cyperus lancastriensis Porter)
Dodder (Cuscuta obtusifora HBK.) growing on Dianthera americana L.

With further deposition Rice Cut-grass appears among the Spike Rush and may even become the dominant plant, forming a Leersia oryzoides (L.) Sw. zone above the Spike Rush. However, the Spike Rush never entirely disappears in the Rice Cut-grass zone in spite of the shade produced by the taller growing plant. An island representing this stage was not present in the area studied, but the Rice Cut-grass zone was present on many of the larger islands where it was studied. On one of these islands, the first one below the Elm Hill Pike bridge, in the Rice Cut-grass zone were found the following plants in small numbers:

Frank's Sedge (Cyperus Frankii Kunth.)
Fowl Meadow Grass (Glyceria nervata [Willd.] Trin.)

All of these plants aid in slowing down the stream and causing deposition. So, the island grows, and as it gets larger and farther above the water table, becomes less fit for the moisture loving Spike Rush and Rice Cut-grass.

Under these conditions a mixture of annuals and perennials comes in and is able to displace the semi-aquatic plants. The annuals are ruderal plants for the most part and are able to come up, grow, and mature a crop of seed after the spring floods. The perennials are those, like the docks, water smartweed, and plantain, that can endure flooding for a long time. The island is not yet high enough to be above the winter and spring floods. The annual-perennial plant zone was dominated by these plants:

ANNUALS:

Spanish Needles (Bidens bipinnata L.)
Spreading Chervil (Chaerophyllum procumbens [L.] Crantz.)
Common chickweed (Stellaria media [L.] Cyrill.)
Three-seeded Mercury (Acalypha virginica L.)
Annual Wormwood (Artemisia annua L.)

PERENNIALS:

Bermuda Grass (Cynodon Dactylon [L.] Pers.)
Jointed Grass (Paspalum distichum L.)
Gattinger's Witch Grass (Panicum Gattingeri Nash.)
Late-flowering Thoroughwort (Eupatorium serotinum Michx.)
Pale Dock (Rumex altissimus Wood.)
Common Plantain (Plantago major L.)
Water Smartweed (Polygonum acre HBK.)
White Heath Aster (Aster ericoides L.)

In addition, other annuals were present in smaller numbers, as follows:

Giant Ragweed (Ambrosia trifida L.)
Ragweed (Ambrosia artemisiifolia L.)
Sneezeweed (Helenium tenuifolium Nutt.)
Dog Fennel (Anthemis Cotula L.)
Venus' Looking-glass (Specularia perfoliata [L.] A.DC.)
Wild Peppergrass (Lepidium virginicum L.)
Lamb's Quarters (Chenopodium atbum L.)
Upright Spotted Spurge (Euphorbia Preslii Guss.)
Barn-yard Grass (Echinochloa crusgalli [L.] Beaw.)
Wire Grass (Eleusine indica Gaertn.)

These perennials and biennials were also found but in smaller numbers:

Thin Grass (Agrostis perennans [Walt.] Tuckerm.) Johnson Grass (Sorghum halepense [L.] Pers.) Red Top (Agrostis alba. L.) Large Buttonweed (Diodia virginiana L.) Common Evening Primrose (Oenothera biennis L.) Tradescant's Aster (Aster Tradescanti L.) Aromatic Aster (Aster oblongifolius Nutt.) Jerusalem Artichoke (Helianthus tuberosus L.) Heal-all (Prunella vulgaris L.) Horse Nettle (Solanum carolinense L.) Red Clover (Trifolium pratense L.) Yellow Dock (Rumex crispus L.) Broad-leaved Dock (Rumex obtusifolius L.) Wild Carrot (Daucus Carota L.) Hoary Plantain (Plantago media L.) White Vervain (Verbena urticaefolia L.) Great Lobelia (Lobelia siphilitica L.) Alsike Clover (Trifolium hybridum L.) Swamp Sunflower (Helenium autumnale L.)

When islands have reached this state it becomes apparent that the down stream part is the youngest, for the stage in plant succession here is younger than elsewhere. While islands of rivers may gain more soil than they lose, the river erodes above and deposits below. As a consequence the islands migrate down the stream, as well as grow in area year by year. Hence the upper part of the island is the oldest, and the lower part the youngest, as the vegetation well shows.⁵ An island representing this condition was studied in the second group of islands about half way down the length of the creek. Here there is a bare sand pit on the extreme lower end of the island, then a zone of annual seedlings. Passing up the island may be found a zone of Spike Rush and Rice Cut-grass; one of

sedges and grasses; and one of annuals and perennials. The velocity of the stream is checked by coming into contact with the island, hence it continues to deposit part of its load on the lower part of the bar. This gives a further foothold for plants to become established.

When deposition reaches the point that the island is above water most of the time—except in extreme floods—trees may get a start and maintain themselves. In the islands studied only five or six had reached the stage where trees had entered. Only these trees were found:

Black Willow (Salix nigra Marsh.)
Sycamore (Plantanus occidentalis L.)
Silver Maple (Acer saccharinum L.)
Green Ash (Fraxinus pennsylvanica lanceolata [Borkh.] Sarg.)

Thus in the normal plant succession on bars and islands in Mill Creek, it is possible to recognize five different plant associations, as follows:

- (1) The Pioneer Willow Herb Association.
- (2) The Spike Rush Association.
- (3) The Rice Cut-grass Association.
- (4) The Annual-Perennial Herb Association.
- (5) The Willow-Sycamore Pioneer Association.

The later stages in the succession are not represented in the area studied, but Cowles⁶ states that after the annuals and willows comes a characteristic flood plain forest. The silver maple (Acer dasycarpum) usually appears with or soon after the willows. After the willows the cottonwood (Populus deltoides) and the ash (Fraxinus americana) soon come in.

Gradually the growing flood plain becomes dry enough to permit the germination and development of a true mesophytic flora. The trees named above, especially the willows, are largely replaced by others that seem better adapted to the changed conditions. Among these are the elms (*Ulmus americana* and *U. fulva*) the basswood (*Tilia americana*), the walnut (*Juglans nigra*), and the pig-nut (*Carya porcina*).

Each plant association prepares the way for the association to follow, and in so doing prepares the way for its own death.

II. PLANT SUCCESSION ON THE CREEK BANK

This section deals with the plant succession on the depositing areas of the creek bank on the south or Knapp Farm side.

One of the earliest stages studied was about a third of the distance down the creek's length by the Knapp Farm. It was a sandy, rocky area. There was no permanent vegetation established near the water's edge, but farther from shore were annuals, perennials, and tree seedlings.

In the summer many seedlings of annuals were found in the damp sandy soil, but practically none of them produce seed; prob-

ably due to the intense shade from trees growing near. These plants were found:

Rice Cut-grass (Leersia oryzoides [L.] Sw.) Frank's Sedge (Cyperus Frankii Kunth.) Lancaster's Cyperus (Cyperus lancastriensis Porter) Fowl Meadow Grass (Glyceria nervata [Willd.] Trin.) Bermuda Grass (Cynodon Dactylon [L.] Pers.) Inland Rush (Juncus interior Wiegand) Yard Rush (Juncus tenuis Willd.) Larger Buttonweed (Diodia virginiana L.) *Clammy Hedge Hyssop (Gratiola virginiana L.)7 Heal-all (Prunella vulgaris L.) Marsh Violet (Viola cucullata Ait.) *Common Plantain (Plantago major L.) *Pale Dock (Rumex altissimus Wood.) Yellow Dock (Rumex crispus L.) Broad-leaved Dock (Rumex obtusifolius L.) *Bearded Day-flower (Commelina hirtella Vahl.) *Day Flower (Commelina communis L.) Blue Mist-flower (Eupatorium coelestinum L.) *Water Smartweed (Polygonum acre HBK.) Late-flowering Thoroughwort (Eupatorium serotinum Michx.) Small White Crown-beard (Verbesina virginica L.) Horse Nettle (Solanum carolinense L.) Red Clover (Trifolium pratense L.) *Frostweed Aster (Aster ericoides L.) *Lady's Sorrell (Oxalis corniculata L.) *Wire Grass (Eleusine indica Gaertn.) Low Spear Grass (Poa annua L.) *Lady's Thumb (Polygonum Persicaria L.) *Common Chickweed (Stellaria media [L.] Cyrill.) Yerba de-tajo (Verbesina alba L.) *Ivy-leaved Morning-glory (Ipomoea hederacea Jacq.) *Annual Wormwood (Artemisia annua L.) Ragweed (Ambrosia artemisiifolia L.) Lamb's Quarters (Chenopodium album L.) Purslane (Portulaca oleracea L.) Horse-weed (Erigeron canadensis L.) *Upright Spotted Spurge (Euphorbia Preslii Guss.) Spanish Needles (Bidens bipinnata L.) Dog Fennel (Anthemis Cotula L.) Wild Pepper Grass (Lepidium virginicum L.) Three-seeded Mercury (Acalypha virginica L.) Cocklebur (Xanthium canadense Mill.) *Crab Grass (Digitaria sanguinalis [L.] Scop.)

Vegetation on these banks still further aids the natural deposition of the stream by slowing it down still further. The American Willow Herb may become established on the outer rim of some of the new bars, especially if the bar is in a sandy spot. The absence of the American Willow Herb on the bar studied above may be correlated with the dense shade present. On the other islands studied the American Willow Herb was the pioneer plant and was followed by the annual-perennial plants as on the islands.

As deposition continues ruderal plants may become very abundant in numbers and kinds, especially if the bank is of sand and exposed to the sun. Such a stage is represented on the Mill Creek bank under and up the stream from the railroad bridge. In the

summer is found a dense growth of tall ruderals, some reaching the height of twelve feet, such as Giant Hyssop (Agastache nepatoides [L.] Ktze.) and Giant Ragweed (Ambrosia trifida L.). This luxuriant plant association is composed of annuals, perennial grasses [L.] Ktze.) and Giant Ragweed (Ambrosia trifida L.). This bank has on it specimens of almost every species of herbaceous plant found on the bank of the creek in the zone between low and high water. The soil is fairly damp because it is at the foot of a slope and water from the slope drains into it. Sunshine is abundant, due to the fact that it faces southwest and trees on the southwest side of the creek and along the railroad right of way have been cut.

Sixty-nine different species of plants were found here. Thirty-nine were ruderal plants; thirty-two, annuals; and thirty-seven per-

ennials. There were no woody plants.

Besides the characteristic plants listed above there were many

others, less abundant, which need not be given here.

This plant society we will call the Annual-Perennial Herb Association. It is frequently the pioneer plant association on a depositing sand bank and in sunshine quickly reaches its climax. When the plants are as luxuriant as just described, they make a very dense shade and practically prevent young trees getting a start here. On this bank tree seedlings were very scarce, these only being found:

Silver Maple (Acer saccharinum L.) Hackberry (Celtis mississippiensis Bosc.) Box Elder (Acer Negundo L.) Sycamore (Plantanus occidentalis L.)

However, on other banks where annual-perennial herbs are not so luxuriant, from the very first appearance of the sand bank, young willow (Salix nigra Marsh.), sycamore (Plantanus occidentalis L.), and cottonwood (Populus deltoides Marsh.) seedlings appear. But they do not persist and grow into trees for presumably they are killed by being covered too long with water in the rainy season. When the depositing bank reaches the point at which it is not covered with water except at the high water stage, seedlings of all these plants can survive. These seedlings have the ability to stand occasional, but evidently not prolonged, submergence.

As these trees grow taller, they shade out the ruderal plants so that they gradually disappear. Meantime their leaves and other remains have increased the humus of the soil. Their place is taken by species more suited to the shade and the moist conditions here

found. Perhaps the most characteristic of these herbs are:

Marsh Violet (Viola cucullata Ait.)
Day-flower (Commelina communis L.)
Lady's Sorrel (Oxalis corniculata L.)
Nettle (Urtica chamaedryoides Pursh.)
Three-seeded Mercury (Acalypha virginica L.)
Satin grass (Muhlenbergia mexicana [L.] Trin.)
Nimble Will (Muhlenbergia Schreberi J. F. Gmel.)

The less characteristic plants need not be given here.

This society of plants will be called the Willow-Cottonwood-Sycamore Plant Association after its most prominent members.

With continued deposition of soil by the stream at high waterand this is greatly aided by the young trees—the bank approaches a height at which it is only covered with water during extreme floods; thus making a flood plain. Under these conditions of moisture and shade, the water maple (Acer saccharinum L.), box elder (Acer Negundo L.), and green ash (Fraxinus pennsylvanica lanceolata [Borkh.] Sarg.) appear. These may be regarded as pioneer flood plain plants. These were found among the sapling willows, poplars, and sycamores wherever the association was studied. With continued soil deposition, though now in small amount and at long intervals apart, the soil becomes so high that it is not suited to germination of willow and cottonwood seed since these are only viable for a short time after ripening and only germinate in moist places. Their young trees do poorly in shade and die off easily. Thus new willow, cottonwood, and sycamore trees do not usually come in to take the place of the older ones. A great many of the older cottonwoods and willows are killed by insects and fungi, so that many dead trees are found in the early flood plain portion of the creek bank. As a result the Willow-Cottonwood-Sycamore Plant Association gives way to the Water Maple-Box-Elder Plant Association of the upper creek bank. This association should give way to a flood plain type of vegetation but the flood plain here is in cultivation. However, there occurs a very small, embryonic flood plain on a terrace about a hundred yards down the creek from the railroad bridge.

Alluvial terraces are accounted for in two ways. First, when a stream with an alluvial flat is rejuvenated, the stream sinks its channel below the level of the flat. The remnants of the old flood plain constitute alluvial terraces. Second, when a stream overflows its banks, its velocity is checked and it aggrades its valley. The mud particles are nearly three times heavier than the water and have a tendency to sink to the bottom and form a terrace.⁸

In all cases where there are several terraces in a valley, one above another, the higher ones are older than the others and represent the level at which the first sedimentary deposits were spread out. The part of the terrace next to the stream is narrower than the portion higher up.⁹

A wire fence is stretched along the lower part of this terrace. Farther down the creek, this fence seems to have caught and held leaves and bits of plant debris which caught and held part of the soil washed down by the rains. This process continued until the fence was well covered, thus making an artificial bank or bench. The most characteristic trees of the terrace were:

White Ash (Fraxinus americana L.)
Catalpa (Catalpa bignonioides Walt.)
Common Locust (Robinia Pseudo-Acacia L.)

White Elm (Ulmus americana L.) Winged Elm (Ulmus alata Michx.) Red Oak (Quercus rubra L.)

Beneath the shade of these trees, shade-loving and tolerating herbs are found in abundance. In the more open spaces the usual type of creek bank plants are still found in profusion. The characteristic shade-loving plants were:

Spotted Touch-me-not (Impatiens biflora Walt.)
Weak Nettle (Urtica chamaedryoides Pursh.)
Pale Persicaria (Polygonum lapathifolium [L.] S. F. Gray)
Goose Grass (Galium Aparine [?] L.)
False Nettle (Boehmeria cylindrica [L.] Sw.)
Indian Pink (Spigelia marilandica L.)
Wood-grass (Muhlenbergia mexicana [L.] Trin.)

In addition to the characteristic trees and shade-loving plants listed above there were many others which are not given here. This association will be called the *Young Flood Plain Plant Association*.

The highest part of the creek bank is covered throughout its length with trees. These trees are tall and have grown close enough together so that there has been much self-pruning. In the ungrazed regions there is an abundance of undergrowth consisting of shrubs and young trees, which will replace the mature trees as they disappear.

The vegetation here makes up the typical flood plain plant association. It is rarely flooded. The characteristic trees of this association are:

Black Walnut (Juglans nigra L.)
White Ash (Fraxinus americana L.)
Redbud (Cercis canadensis L.)
Bur Oak (Quercus macrocarpa Michx.)
Red Oak (Quercus rubra L.)
Black Locust (Robinia Pseudo-Acacia L.)

The most typical plants growing beneath these trees are:

Wood-grass (Muhlenbergia mexicana [L.] Trin.) Small Cane (Arundinaria tecta [Walt.] Muhl.) Ground Ivy (Nepeta hederacea [L.] Trevisan)

The additional trees, shrubs, and herbaceous plants of the Flood-Plain Plant Association are not presented in this paper.

The outermost portion of the upper creek bank merges suddenly into the farm land and contains many herbaceous plants of the cultivated land and meadows. It is the *Tension Zone* between the flood plain forest and the cultivated field and is characterized by a great abundance of ruderal plants, especially giant ragweeds.¹⁰

The essential nature of succession is indicated by its name. It is a series of invasions, a sequence of plant communities. Succession must be regarded as the development or life-history of the climax formation.¹¹ The plant succession on the bank of Mill Creek is essentially as follows:

- I. The Dianthera americana hydrophytic plant association. (Under certain conditions this association may be absent.)
- II. The Annual-Perennial Herb Association.
- III. The Willow-Cottonwood-Sycamore Tree Association.
- IV. The Young Flood-Plain Plant Association.
 - V. The The Flood Plain Plant Association.
- VI. The Tension Zone between the flood plain forest and the cultivated land.
- ¹Contribution No. 1 from the Biological Laboratory of George Peabody College for ers. Presented by the senior author before the Tennessee Academy of Science, Teachers. Presented November 30, 1928.
- ²The junior author did practically all of the field work for this paper under the supervision of the senior author. The junior author is also responsible for the identification of the specimens.
- ⁸The technical names of the plants used here are those given in Asa Gray's New Manual of Botany. Seventh Edition (1908), or, where the plants are not described in Gray, Britton and Brown's An Illustrated Flora of the Northern United States, Canada and the British Possessions.

 - ⁴Salisbury, Rollin D., 1919. Physiography. New York. ⁵Cowles, Henry C., 1901. The Plant Societies of Chicago and Vicinity. Chicago. ⁶Op. cit.
 - ⁷The plants preceded by an asterisk were definitely known to produce seed.
 - 8Cowles, op. cit.
 - Price, George M., 1923. The New Geology, pp. 145-146.
- ¹⁰Herbarium specimens of most of the plants mentioned in this paper have been deposited in the Biological Laboratory of George Peabody College for Teachers.
- 11Fisher, M. L., 1919. The Washed Lands of Indiana. Circ. 90, Purdue Univ. Agr. Exp. Sta.