

## TREND OF SUCCESSION IN A SOUTHERN BOG

E. R. BOGUSCH

*University of Illinois, Urbana.*

Situated within the coastal prairie of Texas and comprising a conspicuous part of the lowland vegetation of its particular locality is a bog whose uniqueness is due to its position relative to climate rather than to its importance as a marsh. Its ecologic position seems to have a bearing upon succession taking place within it as well as to provide extensions in the recorded distribution limits of a typically eastern flora. In all, the bog area is in decided contrast to the surrounding vegetation, for aside from scattered coastal marshes and a few east Texas lowland swamps, the vegetation of Texas bears a decidedly mesophytic stamp. Toward the western part of the state the species of plants are of more and more xeric types with the diminished rainfall. This tendency toward xerophytism is remarkably uniform over western Texas as a whole.

This characteristic of the vegetation of Texas was early recognized by Bray ('99-'06) and later confirmed by the descriptive work of Tharp ('26) in his study of the eastern half of the state. In river bottoms there is a recurrence of eastern types of plants, chiefly herbaceous forms. This is true even as far west as the Trans-Pecos Region, but nowhere has such an abundance of species been recorded in such an apparently stable unit of vegetation of such anomalous distribution as is found in the river bottoms of the San Marcos River in northern Gonzales County a few miles above the river's junction with the Guadalupe River.

A considerable part of the bog area occupies an ancient river flood plain, now far enough above the level of high water during flood periods to escape all but very slight inundation near the river channel proper. Because of the flood plain origin of the area, there is little difference in level except that due to secondary erosion, and this variation in level affords but partial drainage of the area through the overflow channels leading into the river. As a consequence, much of the water entering the area both by rainfall and through seepage is retained and thus helps to maintain the established bog conditions. Local influences enter here and there, and it is from observing the effect of these that the probable trend of succession here recorded has been studied.

## VEGETATION UNITS IN THE BOG AREA

Work on the locality was distributed over four years and was undertaken primarily from a systematic standpoint. Plants were collected as much as possible in their seasonal aspects, and it was from a study of these, their growth forms, and from habitat data that attention was focused upon certain definite changes that were taking place during the period of collection.

Certain vegetation units have been separated from each other, chiefly on the basis of dominant species in combination with physiographic factors. Briefly they are as follows: The ash swamp, the sphagnum bog, the quaking bog, and the hay meadow. They will each be described in detail.

## THE ASH SWAMP

From the accompanying map, it can be seen that this is the largest homogeneous unit of lowland vegetation. The ash swamp is an alluvial forest occupying an old river flood plain but extending up the adjacent sandstone slopes to a short distance. The soil consists of clay, sand, and dark organic matter and burns to a reddish mass with much the hardness and feel of brick. No soil except that of this particular unit of vegetation has this tendency to thus cohere and fuse.

There is a shallow drainage system of small interlacing channels within the bog. During a part of the year they contain no water except for brief periods after heavy rains. At other seasons they are full and overflowing. These seasonal variations in water table constitute an interesting problem in themselves. The natural contour of the bottoms is such that with the exception of the bogs proper, comparatively few parts serve as retention basins; and although the run-off is gradual, the effect of rain ponds because of their limited size is slight. Where such ponds exist the woody vegetation is reduced, which seems to indicate their already long existence. The three most important of them occurring in our area have been designated by circular enclosures on the map.

The periodicity of the water table presents an interesting phenomenon. The time of maximum inundation of the swamp area is during winter and early spring. This becomes less pronounced as the season progresses and reaches an approximate minimum during mid-summer. During late fall and early winter the rise of the water table can be readily observed by the increasing wetness

of the top layers of soil, which condition reaches a maximum at mid-winter. Because of the rough coincidence with changes in the development of the leafy canopy the theory that leaf transpiration plays an important part in reducing the ground water has been advanced several times by workers in the field. However, there is no evidence to substantiate this assumption. The importance of this periodicity lies in its effect upon successional sequence in the parts of the swamp where the most rapid changes are taking place.

In addition to comprising the largest part of the bog area, the ash swamp represents the largest single aggregation of ash trees of this species anywhere west of the east Texas river bottoms. Toward the eastern border of the wooded flood plain, contact is made with the sphagnum bog, which in turn meets the slope of the sand hills adjacent to it. On the west and also on the south the river terminates the vegetation except where cultivation has been practiced. It is near the southwestern corner of the flood plain that the hay meadow previously mentioned occurs. On the north, contact is made with the quaking bog.

*Fraxinus pennsylvanica* is the dominant species of the ash swamp except in marginal situations. Here grows a generous mixture of *Quercus macrocarpa*, *Quercus rubra*, and *Quercus shumardii*. These three along with scattered small ash trees grade into and give way to the sand hill dominants of *Quercus stellata*, *Quercus marilandica*, and *Carya sp.* On the other hand, where the sphagnum bog is intermediate in position between the ash swamp and the uplands, *Quercus macrocarpa* is the chief forest tree, mixed with numerous saplings of *Salix nigra* and *Populus deltoides*. The only tree of *Quercus alba* observed in the entire region of northern Gonzales County occurs here in this transition zone. In the more open parts of these marginal areas, occasional trees of *Fagora clava-herculis* and *Sapindus drummondii* are mixed with the common river bottom *Celtis mississippiensis*. Such trees as the last mentioned three exhibit a peculiarity of bark structure that appears to be due to the crowding effect of the other trees. Instead of the customary roughness, the bark in most instances resembles that of the beech in smoothness with but minor irregularities. The growth habit is also modified so that the trees are slender and tall instead of having the normal low spreading habit.

The understories are of two general classes. The first includes those lianas that reach the level of the arboreal canopy and include robust forms such as *Campsis radicans*, *Parthenocissus*

*quinquefolia*, *Ampelopsis arborea*, and *Ampelopsis cordata*. The others make up a distinct layer and include the smaller lianas and the characteristic undershrubs of the forest. *Smilax renifolia* and *Berchemia scandens* along with certain unimportant species are the more common of the smaller scandent forms and in many cases nearly cover the small trees in more open spots. Among the trees of this second system of layering are *Ilex vomitoria* and *Ilex decidua*, *Morella cerifera*, and *Ulmus alata*. Occasionally a third and lower layer of *Sabal glabra* and *Aesculus pavia* occurs. In some of the better lighted parts of the ash swamp occasional trees of *Crataegus texana*, *Rulac texana*, *Svida asperifolia*, *Sambucus canadensis*, and *Viburnum rufotomentosum* are to be found in the second system of layering. Of these *Crataegus* and *Sambucus* are practically the first to flower in the early spring and are conspicuous enough to deserve mention.

A possible fourth layer may be distinguished in the epiphytic plant of *Dendropogon usneoides*, commonly called Spanish Moss. This is of unusual abundance on the trees of the lowlands and rapidly disappears on the trees of the adjacent slopes, where it is replaced by the more xeric species, *Tillandsia recurvata*. The former species occurs on both ash and oak up to the tops of the lower trees. It is apparently terminated both by the light intensity and the drying effect of winds that sweep over the tops. On the other hand, unless removed by browsing animals, the epiphyte extends almost to the ground in many places. Thus, if we may properly speak of this plant as comprising a layer, we have one of unusually wide vertical distribution.

During the early spring before the leafy covering develops to any considerable extent, two types of ground vegetation exist. One is aquatic and depends upon the presence of the high water table and disappears simultaneously with the lowering of the water level. The other is terrestrial and the normal herbaceous covering composed of early maturing plants, most of which are perennials.

The aquatic species are few, *Callitriche heterophylla* and *Potamogeton lucens* being those most abundant. In addition, such mud loving plants as *Iris hexagona*, *Juncus effusus*, *Onosmodium bejariense*, and *Muricauda dracontium* skirt the borders of the drainage channels. The *Iris* is found scattered in several places, nowhere abundantly. *Muricauda* is even more widespread but scarcely more common. It is among the first plants to send up its leaves, later also producing the flowering spathes. The leaves soon

die, and upon the maturing of the fruit the stalks fall over, leaving the red berry-like fruits to be spread by birds and whatever means may afford.

*Muricauda*, *Iris*, *Sanicula canadensis*, *Geum canadense*, and *Amsonia amsonia* are the most common perennial spring herbs. These mature their activities by early summer. Among the common annuals are *Bowlesia septentrionalis*, *Cardamine arenicola* and *Cardamine pennsylvanica*, *Galium aparine*, *Poa annua*, *Myosotis virginica*, and *Senecio lobatus*.

By early summer, species of *Persicaria*, *Cardiospermum halicacabum*, and *Willughbaeya scandens* take complete possession of the border areas and such open spots as may exist. These marginal areas grade into comparatively broad flats of *Diodia teres* that lie between the ash swamp and the quaking bog on the north and the sphagnum bog on the east. In these interrupted transition zones, such woody plants as *Morella*, *Ilex* and *Baccharis sp.* may be found.

Under the trees the vegetation in summer is restricted to typical shade loving plants as *Heliotropium indicum*, *Saururus cernuus*, *Oplismenus setarius*, and *Polymnia uvedalia*. The fewness in numbers and the small size of some of these species contribute but little to the effectiveness of the ground cover. *Saururus* is more gregarious in the better lighted situations, while *Heliotropium* occurs here and there along the drainage channels.

#### THE SPHAGNUM BOG

The sphagnum bog is the smallest unit of the vegetation here considered. It lies east of the ash swamp in a narrow zone running north and south and is fed by seep water that in several places comes forth with sufficient volume to produce flowing springs. Considerable quantities of peaty material belonging to the decay of the older sphagnum moss and small amounts of sand make up the soil. Thus, even when the water table is low enough to allow surface dryness in the ash swamp, sufficient water is retained by the subsoil of the sphagnum bog to permit such plants as would perish by complete drying to persist. The sphagnum moss finds itself here at its known southwestern limit in the United States, as far as available published data is concerned. Prior to its discovery in the bogs here, the known limit was in the river bottoms of east Texas. Thus a few hundred miles extension of range is hereby added.

The several dominants are difficult to determine because of the decidedly seral nature of the bog. On practically all open wet sandy flats, *Monniera monniera* and *Hydrocotyle ranunculoides* form mats that are characteristic of the situation, exercising a degree of control so effective as to exclude practically all other plants. More centrally located are *Sagittaria falcata*, *Andropogon glomeratus* on minute hummocks of its own making, and *Typha latifolia*.

Boundary lines are nowhere sharp except where minor topographic conditions permit. In general there is more or less complete grading of herbaceous forms from sphagnum bog to ash swamp until excluded by light, and the woody species of the latter form a sinuous line where the two units make contact. Of these trees, *Salix nigra*, *Ilex decidua* and *Ilex vomitoria*, *Prunus mexicana*, *Morella cerifera*, and *Aesculus pavia* may be looked upon as indicative of the transition. *Morella* seems more tolerant of varying soil and light conditions and therefore forms the broader band included within the two units of vegetation.

Seasonal changes give a more varied floristic appearance in the sphagnum bog than is to be expected in the ash swamp. The prevernal period is one of winter rosettes and seedling plants. Active growth from perennial roots and rootstocks comes later in the season than does that of the seedlings of such species as *Chaerophyllum teinturierii*, *Cardamine arenicola*, *Commelina nudiflora*, *Persicaria hydropiperoides*, *Ptilimnium capillaceum*, *Poa annua*, and species of *Cyperus* and *Eleocharis*. The rosettes of *Samolus floribundus*, *Carduus muticus*, and *Cicuta maculata* begin development later in the season.

The first pronounced changes come during the latter part of February and early March. Among the first plants to bloom of the above mentioned species are *Cardamine*, *Chaerophyllum*, *Ptilimnium*, and *Commelina*. These are followed by *Ipomoea speciosa*, *Jussiaea suffruticosa*, *Monniera*, and *Sagittaria*. *Wilugbaeya scandens* comes into flower at the end of the season along with the sedges.

With the coming of summer the greatest percentage of conspicuous flowers are in bloom, and of these *Jussiaea*, *Commelina*, and *Monniera* persist with additions of *Conoclinium coelestinum*, *Lobelia splendens*, *Carduus muticus*, *Helianthus strumosus*, and additional species of *Persicaria*. Most of these continue until fall with few changes.

## THE QUAKING BOG

The quaking bog closely resembles the sphagnum bog, at the same time representing an apparently more mature stage. The substratum is also of high water retaining capacity and in addition to the decayed organic mass there is during the time of greater soil water a distinct layer of ooze, lacking in the sphagnum bog. It is the floating effect of the superimposed material that gives the bog its quaking nature during a part of the year. On the other hand, the quaking bog, because of its limited extent, is in no way comparable to those large bogs of the north, for it has no great depth, and during the dry period much of the quaking disappears. A pond of open water lies in the center, and in this the water, too, recedes periodically, leaving a mud bottom with its incidental vegetation until the next period of flooding.

Sedges exercise control with grasses as apparent invaders. The soil consists of much of this decomposed sedge material in addition to the remains of sphagnum which appears sparingly in the more sandy places. From the pond-like depression in the center, a shallow ill defined drainage channel carries the overflow water westward into the river.

Two species of *Eleocharis* exercise control. Of these, *Eleocharis interstincta* occupies the pond-like depression proper with the exception of the very center and terminates abruptly at the water level with a rapid change to *Eleocharis tortilis*.

From the center of the pond northward the following zones may be described:

100 foot zone of *Daubentonia longifolia* and *Eleocharis interstincta*.

120 foot zone of *Eleocharis tortilis*.

100 foot zone of *Morella*, *Ilex*, and *Baccharis*.

30 foot zone of *Pteridium aquilinum*.

From this point cultivation is begun and the nature and extent of the natural vegetation lost. From the center of the pond southward the zone of *Eleocharis tortilis* makes contact with a broad zone covered with *Diodia teres* in summer on which occur such woody species as *Ilex vomitoria* and *Ilex decidua*, *Salix nigra*, and *Morella cerifera*.

The seasonal changes present here the greatest riot of color. Winter rosettes are of the same species as found in the sphagnum bog. *Cicuta* is scarce and *Carduus muticus* has not been reported.

In the summer the bog is in its most colorful condition. *Bidens frondosa* and *Bidens nashii* begin to bloom and continue throughout the summer. *Conoclinium coelestinum*, *Pluchea camphorata*, *Isnardia palustris*, *Ludwigia glandulosa* and *Ludwigia alternifolia*, *Jussiaea suffruticosa* and *Jussiaea diffusa*, and *Rhexia mariana* add to the display. A single orchid, *Habenaria repens*, has been reported. During the fall most of these same species continue, and *Willugbaeya scandens* often completely covers low shrubs and small trees. Among the grasses, *Andropogon glomeratus* and *Andropogon virginicus* are conspicuous along with *Sporobolus buckleyi*.

A very interesting secondary sere is initiated in the pond-like basin during the dry period. Upon this bare area *Hemicarpha micrantha* and two grasses, *Eragrostis hypnoides* and *Paspalum sp.* establish themselves. Seed matures and sheds before the ground becomes flooded again.

Invaders are practically excluded in the sedge zone because of the density of the stand and unfavorable conditions for ecesis. The shade under the sedge cover is very dense as are also the mats of rhizomes. Both operate effectively to exclude invaders. The introduction of cattle has through injury of the sedge covering enabled *Salix*, *Fraxinus*, and *Populus* to establish themselves. Ring counts indicate that these invaders have been established for several seasons and seem capable of maintaining themselves successfully.

#### THE HAY MEADOW

This is a small unit much disturbed by mowing and apparently reduced in size by the cultivation of parts of it. Three grasses dominate. They are *Spartina gracilis*, *Paspalum glabratum*, and *Panicum virgatum*. The stand of these grasses is so dense that practically no other vegetation enters except a few plants of *Acuan illinoiensis*.

#### TREND OF SUCCESSION IN THE BOGS

The general trend of succession may proceed in three directions. The most direct and the one that seems the normal one is from sphagnum bog to ash swamp and from there to *Ilex-Myrica* and finally to the upland climax of *Quercus-Carya*. This is indicated by the effect of a winter and spring hydroperiod accompanied by practically dry soil on the partly silted-in margins

during late summer and fall. This dryness kills the sedge and sphagnum covering and creates a bare area suitable for ecesis of the ash seedlings. Such seedlings are not very abundant but are of various ages on these silted-in areas. The ash swamp is a stage of long duration, as can be determined by the large size of some of the ash trees found within it. In addition to these large trees, others of similar proportions mostly of *Populus* along with large specimens of *Quercus macrocarpa* and *Quercus shumardii* give every indication that this seral stage is one of already long existence.

Where rain washes cause rapid silting of portions of the sphagnum bog a succession follows that seems ultimately to result in the *Spartina-Paspalum-Panicum* meadow. This is also an almost static stage, for the density of the grass prevents woody species invading and from successfully competing. Where these silted-in areas of the sphagnum bog are flooded periodically by the rising water table during winter and spring, bare areas are produced that allow *Salix* and *Populus* to enter and be finally followed by *Fraxinus*. The crowding of the first invaders of woody species decimate the numbers until the distribution approaches in appearance that of the existing portions of the ash swamp. As the trees increase in size, only the tallest survive.

In the elevated parts of the grass meadow where the maximum hydroperiod is shorter and comes during the months of root dormancy, the grass responds by rapid growth. In its best expression, both *Panicum* and *Paspalum* reach a height somewhat above the head of an average sized man, while the *Spartina* rarely exceeds three feet at most. Mowing apparently has no further effect than that suggested above, of reducing the number of perennial herbs and making the exclusion of woody invaders complete. Close grazing works an elimination of the grasses and initiates a secondary sere characterized by the overgrazing indicators of *Dichrophyllum marginatum* and *Helenium tenuifolium*. This is contrasted with the sere initiated by cultivation and later abandonment. This latter begins with *Ipomoea trifida* and is followed for a number of years by *Iva ciliata* and *Ambrosia aptera*, and still later by woody invaders of *Salix*, *Populus*, and *Fraxinus*, which seems to indicate a return to the ash swamp conditions. The ash swamp, thus, seems to be the major seral stage preceding the climax and the one to which most other successful stages tend to go.

All three species of grasses yield to cultivation readily. *Spartina*, however, resists midsummer grazing better than either of the other two because of the unpalatable condition of the leaves. These early become sharp pointed and impalatable. The repeated injury to the rhizomes under the hoofs of the animals causes this grass to finally yield with the rest. Early spring grazing, on the other hand, effects all three alike. Heavy grazing in all cases prevents seed production and aids extermination through destruction of rhizomes either by starvation or mechanical injury. With the removal of the grasses, *Dichrophyllum* and *Helenium* enter.

Where the sphagnum bog receives no silt from rain washes and has but a brief winter hydroperiod, the succession normally goes to the *Eleocharis tortilis* stage. Because of the stabilizing effect of the sedge mats, the underlying organic ooze, composed chiefly of partly decayed sphagnum along with other plant remains, becomes covered with a more substantial covering. This forms a quaking bog with a semi-fluid substratum.

If, on the other hand, as in some portions of the bog, the maximum hydroperiod is during both winter and spring because of retention of a part of the water and is never followed by absolute soil dryness during the summer, the stage will be *Daubentonia longifolia* and *Eleocharis interstincta* of such abundance as to practically fill the pond-like depressions up to a depth of water of three feet. Through the accumulation of soil and debris brought in by rains and through the deposition of plant remains this stage will no doubt yield to that of *Eleocharis tortilis*.

Where silting continues slowly the succession goes gradually into *Sporobolus-Andropogon* associates, into which *Pteridium aquilinum* comes in the more compact and better drained soils. Such banks of fern show considerable invasion by *Ilex* and *Myrica* and give every indication of being in the direct successional sequence. If the silting takes place rapidly, as has been the case in some instances where an entire *Eleocharis* bog has been silted-in by rains, *Axonopus compressus* covers smooth flats, entirely devoid of ligneous vegetation. In fact, practically no invaders occur in this carpet grass stage. *Pteridium* tends to invade marginally and gives evidence of securely holding the ground thus gained by the creeping rhizomes. *Axonopus* is eliminated by too much shading, and the fern gradually pushes farther into the carpet grass flat.

Such instances of silting of the quaking bog, as just mentioned, must take place rapidly to have the effect observed. Information

from farmers of the adjoining region reveals that one of the carpet grass flats examined has been produced within the last forty years; and an old wagon road that now passes directly over it has been pointed out as following a more circuitous route before silting-in took place. Whatever the duration of these flats, the succession seems ultimately to go to *Pteridium*, then to *Ilex-Myrica*, and then to the upland climax.

The two directions of succession given above seem to be those normal to the quaking bog. Cattle, however, initiate conditions that show a trend toward the conditions of the ash swamp. Grazing itself has little effect upon the *Eleocharis* mat, for the stems are tough and difficult to get. The chief injury to the mat is due to the breaking of the cover by the animals' hoofs. Upon bare areas thus produced, seedlings of *Populus*, *Salix* and *Fraxinus* have become established in great numbers. Ring counts of the larger ones showed that the invaders were in their fourth growth season during the summer of 1928, and every evidence suggests permanency of these plants. Where such woody species enter and successfully compete, ash bog conditions will probably represent one stage of the sere leading to the upland climax.

With reference to biotic factors in the ash swamp itself, it is significant to note that although *Quercus shumardii* is repeatedly found as seedlings, those of *Quercus macrocarpa* are practically never encountered. This condition depends chiefly upon the activity of the squirrels, who seem to prefer the larger acorns of *Quercus macrocarpa* to those of *Quercus shumardii*. Within two weeks of the falling of the acorns, practically none are to be found. Those of *Quercus shumardii* are present in abundance. This almost complete destroying of the seed crop must ultimately tend to greatly reduce if not eliminate this oak, for with age and injury through other natural causes a certain number of these trees die each year. With the loss of the seed through squirrel activity no new individuals can become established.

#### NEW RANGE LIMITS FOR CERTAIN SPECIES

The taxonomic study of the plants of the region has revealed a number that are out of their reported range. Those not previously reported for Texas are here recorded. At present too little is known of the distribution of species within the state itself to make any comment concerning those species that have been pre-

viously reported for Texas but which have not been encountered this far west before. They are, consequently, omitted.

In making this list, Small ('13) has been used as the authority. This has, however, been supplemented in all cases by consulting the work of Coulter ('91-'94) and that of Wooton and Standley ('15). The species are listed in alphabetic order with the name of the state denoting the limit of southwestern distribution following.

- Anchistea virginica* (L.) Presl. Louisiana.  
*Bidens laevis* (L.) B. S. P. Georgia.  
*Cardamine arenicola* Britt. Tennessee.  
*Cardamine pennsylvanica* Muhl. Missouri.  
*Erianthus compactus* Nash. Tennessee.  
*Geum canadense* Jacq. Missouri.  
*Habenaria repens* Nutt. Louisiana.  
*Helianthus strumosus* L. Arkansas.  
*Monarda fistulosa* L. Louisiana.  
*Lorinseria areolata* (L.) Presl. Louisiana.  
*Pieris mariana* (L.) B. & H. Arkansas.  
*Panicum jorii* Vasey. Louisiana.  
*Persicaria hirsuta* (Walt.) Small. Georgia.  
*Phalaris angusta* Nees. Louisiana.  
*Tradescantia brevicaulis* Raf. Missouri.  
*Xyris caroliniana* Walt. Louisiana.

#### SUMMARY

1. The bog vegetation is surrounded by a vegetation of a decidedly xeric nature and is isolated by wide and impassable barriers from vegetation of a similar nature.
2. The ash swamp presents the densest stand of ash trees found anywhere within the state of Texas.
3. The bog conditions as a whole present an edaphic climax that nevertheless shows definite successional tendencies.
4. The normal succession appears to be from sphagnum bog to ash swamp, where there is an early summer hydroperiod and fall drought. The succession tends to end in the upland climax.
5. Silting of the sphagnum bog allows meadow grasses to come in and thus temporarily diverts the succession into a moist meadow.

6. A short winter hydroperiod favors the formation of miniature quacking bogs on areas formerly occupied by sphagnum bogs, due to a semi-floating mat of sedge. Flooding to a greater degree causes a temporary hydrosere that returns finally to the sedge mat condition. The normal succession goes to *Ilex-Myrica*, as a final stage before the invasion of upland dominants. Silting produces minor changes within the sere itself.

7. Cattle by breaking the sedge mat favor the invasion of ash, cottonwood, and willow and divert the succession into the ash swamp.

8. Minor biotic factors indicate that the suppression of *Quercus macrocarpa* by the destroying of seed will lead to the final elimination of this species.

9. The published distribution of a number of species found in the bog area is here extended.

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