ECOLOGICAL INTERPRETATIONS OF THE VEGETATION PATTERNS OF VOLO BOG, LAKE COUNTY, ILLINOIS

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ABSTRACT.—The vegetation patterns of a sphagnum bog in northeastern Illinois were studied. Quantitative data were collected on cover, density and basal area of woody plants and cover of herbs along transects through all vegetation types. Five primary and two minor vegetation types were delineated. A floating mat composed of herbs and mosses surrounded and advanced on an open pool. Shrubs and then tamaracks invaded the mat. Shrubs present with the tamaracks persisted indefinitely while the tamaracks failed to reproduce, giving rise to an extensive secondary shrub community beyond the coniferous forest. Evidence for transition of the tamarack forest or secondary shrub vegetation to mesophytic forest, as reported in the literature, was not observed. The two minor vegetation types, aspen groves and parklands of poison sumac, did show a closer relationship to surrounding mesic vegetation, but appeared to be edaphically rather than successionally determined.

The Woodfordian Substage of the Wisconsinan glaciation produced the Valparaiso Moraine, a prominent upland complex encircling the southern end of Lake Michigan. In western Lake County and eastern McHenry County, Illinois, and adjacent areas, this moraine is composed of much waterworked sand and gravel and is marked by an abundance of kettles. These depressions are occupied by lakes, bogs and marshes. One of the most biologically interesting of these areas is Volo (Sayer) Bog. This bog

FIGURE 1.—Aerial view of bog from south.

is two miles northwest of Volo, Lake County, in the NE 1/4 Section 28, T. 45 N., R. 9 E. of the Grays Lake Quadrangle. The bog is under the auspices of the Illinois Nature Preserves Commission and the State Department of Conservation.

Volo Bog (Fig. 1) first was described by Waterman (1921, 1923, 1926) and since has been used widely for research and as a resource area for professional and amateur naturalists. Classical bog succession, as described by Whitford (1901), Transeau (1903, 1905), Dachnowski (1912), Cooper (1913), and others, is graphically illustrated in parts of Volo Bog. Despite intensive use of this bog, the vegetation is described only superficially. No quantitative vegetation analysis is available.

The authors' familiarity with the bog, spanning a period of several years, and the study described here give rise to a more complete and somewhat different description and interpretation of vegetation than previous studies by Waterman (1921, 1923, 1926), Kurz (1928), Reichle and Doyle (1965), and Reichle (1969). Because striking vegetation changes have occurred since Waterman's studies and increasing disturbance and development of the surrounding area threaten to further alter conditions in the bog, it is important that information be summarized at this time. Our study, in addition to providing a detailed analysis of a bog, indicates trends in bog succession not generally suggested in the literature.

General Description

Volo Bog occupies a reniform depression oriented nearly north and south between prominent till ridges. The depression consists of two basins (Artist, 1936). The smaller northern basin is completely peat-filled; the larger southern basin still exhibits a small area of open water. It is the southern basin that so prominently displays successional zones. Hydrarch bog succession is well described (e.g. Whitford, 1901; Transeau, 1903, 1905; Cooper, 1913; Dachnowski, 1912, 1924; Dansereau and Segadas-Vianna, 1952), and we do not attempt to review it here. The vegetation patterns exemplified in Volo Bog should be familiar, at least in part, to most students of ecology.

The southern basin exhibits five primary vegetation types and two minor types. The open pool, approximately 40 m. long by 25 m. wide (Fig. 2), is surrounded by a floating mat varying from a few to 60 m. in width. Invading the mat is a shrub community, which in turn is replaced by a tamarack (*Larix laricina* (DuRoi) K. Koch.) forest. Surrounding this forest is a second, more extensive shrub community. These bog associations abruptly give way to a marsh at the periphery of the depression. These five vegetation types occur in roughly concentric zones around the central pool. Scattered irregularly in the edge of the outer shrub community are two less extensive but significant communities, one dominated by poison sumac (*Rhus vernix L.*) and the other by quaking aspen (*Populus tremuloides* Michx).

The substrate in the southern basin is a layer of Sphagnum peat less than one meter in thickness overlying Carex peat (Artist, 1936). Live Sphagnum is abundant at the surface. In the northern basin, however, Sphagnum is greatly restricted and the surface layer is largely woody peat greater than two meters in thickness; Carex peat also occurs under the woody peat (Artist, 1936).

Vegetation of the two basins is similar in aspect, although details of composition differ. Succession in the northern basin evidently is much farther advanced; the open pool as well as the herb mat vegetation is absent. Tamaracks in the northern basin were cut prior to Waterman's first study (1921). Furthermore, *Rhamnus fragula* L., an Eurasian species naturalized in eastern United States, has obliterated virtually all of the original vegetation patterns except the second-growth tamaracks. For these reasons, it is difficult to determine the successional patterns. Presence of woody peat further complicates interpretation. A brief description is included, however, be-

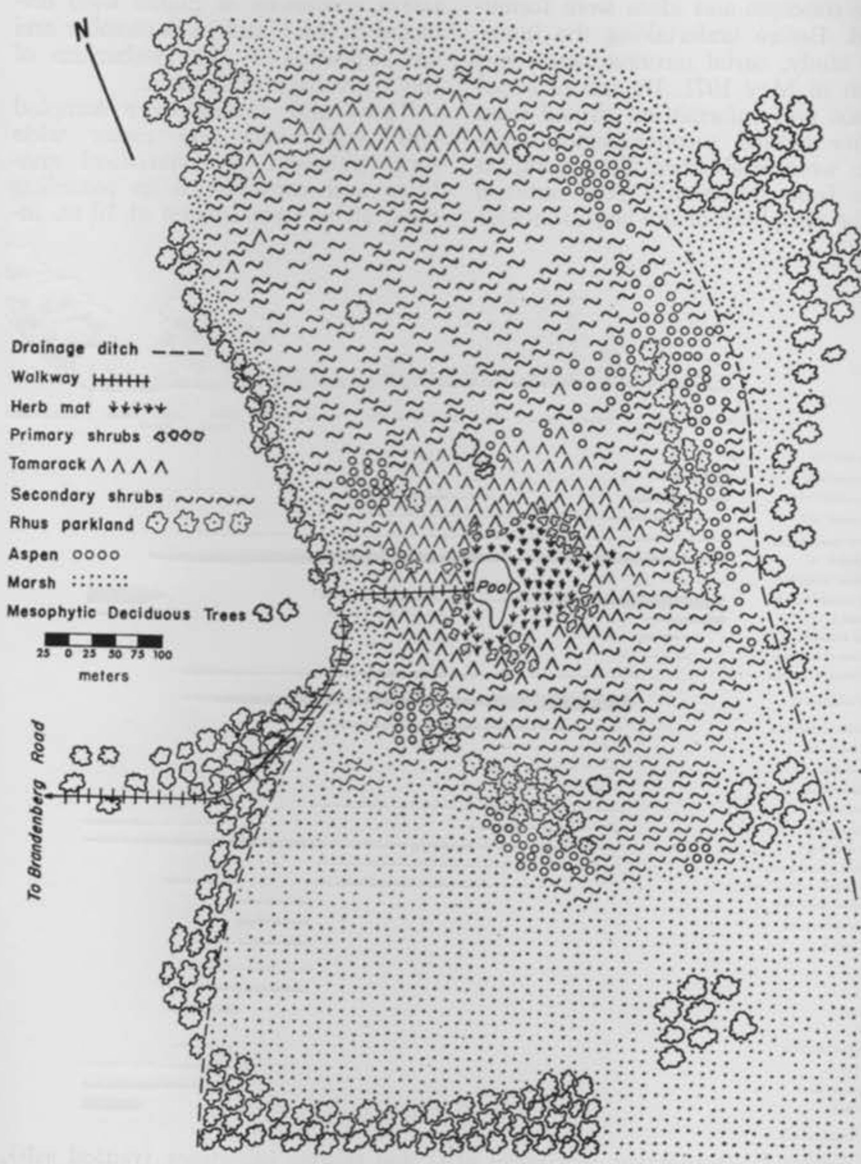

FIGURE 2.—Schematic interpretation of vegetation of Volo Bog.

cause some conclusions are supported by patterns in the northern basin.

Methods

The bog was visited frequently over the past several years during which time concepts and ideas were formulated. Before undertaking the intensive study, aerial reconnaissance was flown in May 1971. By use of aerial photos and information gained from earlier ground reconnaissance, transects were established along compass lines from the central pool outward to the periphery of the bog to include all sections of the bog and all vegetation types. Vegetation in the pool and upland forest was not sampled. Data were collected 24-27 June 1971 along four primary transects that totaled 1040 m. in length. Representative specimens of plants were collected in June and in September and are deposited in the Herbarium of the University of Illinois.

Trees and shrubs were sampled with continuous one meter wide strip transects. For statistical analyses and convenience in recording data, strips were broken at 10 m. in-

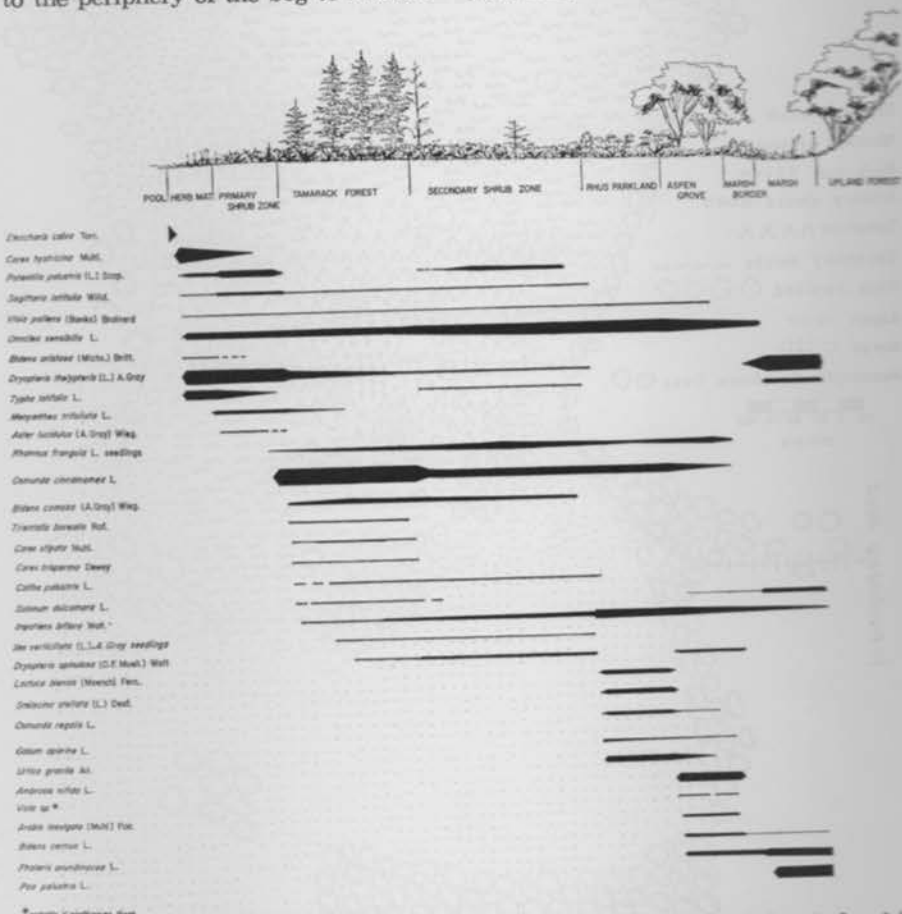

Figure 3.—Distribution (horizontal axis) and relative importance (vertical axis), based on cover and frequency, of herbs in Volo Bog with mean cover greater than one percent in the vegetation type where the species most frequently occurred.

tervals. Density of shrubs was based on clump tallies. Cover was estimated by line intercept along one edge of the strip. Diameters of all trees greater than 2.5 cm. dbh were measured. Herbs were sampled at 5 and 10 m. intervals along the transects, frequency of sampling being determined by uniformity and extent of the community. Cover for herb species was visually estimated in ½ x ½ m. quadrats. The stoloniferous growth form of most herbaceous species negated the significance of density; therefore, counts were not made.

Based on the data and field observations, data were compiled and statistically analyzed according to vegetation types. Data from plots falling on transitions were examined separately.

Vegetation Analysis

Figure 3 diagrammatically presents the distribution (horizontal axis) and relative importance (vertical axis) of all herbaceous species which occur with mean cover greater than one percent in at least one community. Woody species (Fig. 4) necessarily are graphed on a different arbitrary importance scale. The diagram in

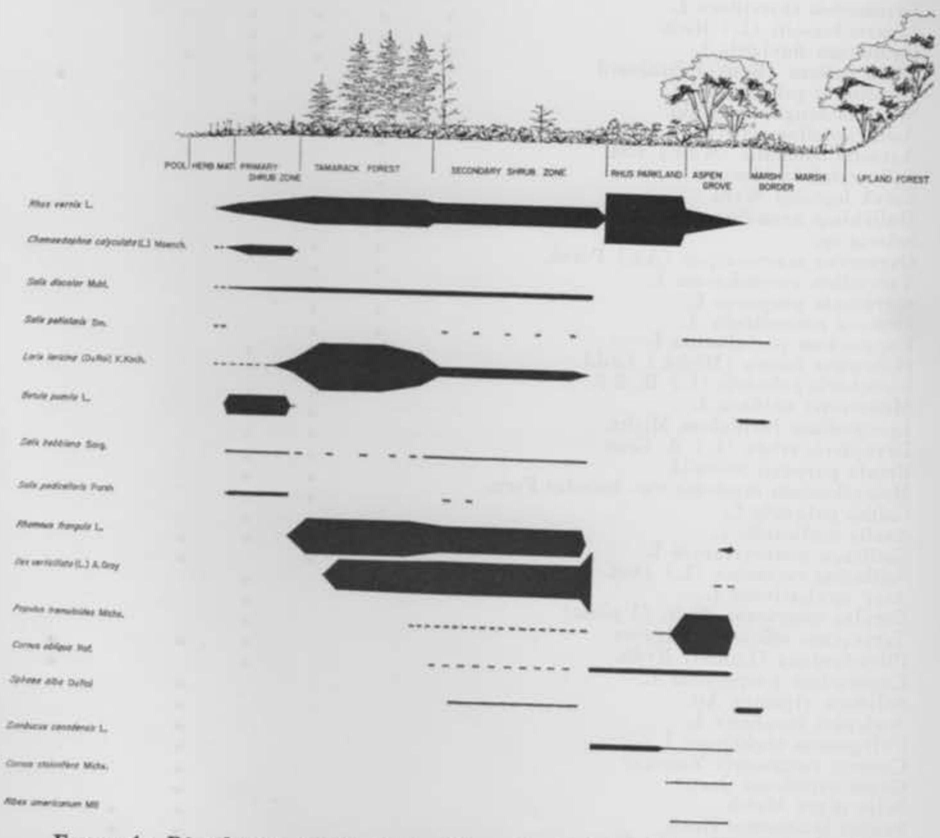

Figure 4.—Distribution (horizontal axis) and relative importance (vertical axis), based on cover, frequency and basal area, of woody plants in Volo Bog with mean cover greater than one percent in the vegetation type where the species most frequently occurred.

TABLE 1.—Species observed or sampled, having less than one percent cover for their indicated habitat.

Species	Herb mat	Primary shrubs	Tamarack	Secondary shrubs	Rhus parkland	Aspen	Marsh
Sparganium eurycarpum Engelm.	*						
Scripus cyperinus (L.) Kunth	*						
Eriophorum angustifolium Nutt.	*						
Glyceria striata (Michx.) Trin.	*						
Calamagrostis canadensis (Michx.) Beauv.	*						
Galium tinctorium L.	*						
Polygonum punctatum Ell.	*						
Epilobium leptophyllum Raf.	*						
Oxypolis rigidior (L.) Raf.	*	*					
Phragmites communis Trin.	*	*					
Triadenum fraseri (Spach) Gleason	*	*					
Lycopus americanus Muhl.	*	*					
Rumex verticillatus L.	*	*					
Pogonia ophioglossoides (L.) Ker.	*	*					
Carex lasiocarpa Ehrh.	*	*					
Lysimachia thyrsiflora L.	*	*	*	*			
Liparis loeselii (L.) Rich.	*	*	*	*			
Equisetum fluviatile L.	*	*	*	*	*		
Viola pallens (Banks) Brainerd	*	*		*			*
Scutellaria galericulata L.	*			*			
Stellaria longifolia Muhl.	*			*			
Aster junciformis Rydb.		*					
Agrostis hyemalis (Walt.) BSP.		*					
Salix candida Fluegge		*					
Carex leptalea Wahl.		*					
Dulichium arundinaceum (L.) Britt.		*					
Scleria sp.		*	*				
Oxycoccus macrocarpus (Ait.) Pursh.		*	*				
Vaccinium corymbosum L.		*	*				
Sarracenia purpurea L.		*	*				
Drosera rotundifolia L.		*	*				
Eupatorium perfoliatum L.		*	*	*			
Habenaria lacera (Michx.) Lodd.			*				
Eleocharis palustris (L.) R. & S.			*				
Monotropa uniflora L.			*	*			
Lycopodium lucidulum Michx.			*	*			
Dryopteris crista (L.) A. Gray			*	*			
Betula purpusii Schneid.			*	*			
Maianthemum candense var. interius Fern.			*	*			
Caltha palustris L.			*	*			
Aralia nudicaulis L.			*	*	*		
Saxifraga pennsylvanica L.			*		*		
Smilacina racemosa (L.) Desf.				*			
Acer saccharinum L.				*			
Corylus americana Walt. (1 plant)				*			
Taraxacum officinale Wiggers				*	*		*
Pilea fontana (Lunell) Rydb.				*			*
Eupatorium purpureum L.					*		
Solidago gigantea Ait.					*		
Asclepias incarnata L.					*		
Polygonum sagittatum L.					*		
Cuscuta campestris Yuncker					*		
Geum canadense Jacq.					*		
Salix nigra Marsh					*	*	
Smilax lasioneura Hook.					*	*	
Lactuca biennis (Moench) Fern.					*	*	
Acer negundo L.						*	
Betula papyrifera Marsh.						*	
Betula lutea Michx. f.						*	
Lobelia siphilitica L.						*	
Cicuta bulbifera L.						*	*
Echinocystis lobata (Michx.) T. & G.							

these figures represents an idealized cross section of the southern basin of the bog along one radius from the central pool. All data for each community were combined for analysis and interpretation. All other species observed or sampled are listed in Table 1.

As can be seen from Figures 3 and 4 and Table 1, the floating mat is composed of many herbaceous species with a few scattered shrubs and tamaracks invading in the older portions. The mat consists of a matrix of roots and mosses, especially *Sphagnum recurvum* Beauv. (Reichle and Doyle, 1965; Reichle, 1969). *Eleocharis calva* Torr. initiates mat formation. Away from the pool, several species assume importance. Dominant species include *Carex hystricina* Muhl., *Dryopteris thelypteris* (L.) A. Gray, *Typha latifolia* L., and *Onoclea sensibilis* L.

Invading the outer portion of the herb mat is a shrub community of *Rhus vernix, Betula pumila* L., and *Chamaedaphne calyculata* (L.) Moench. Of lesser importance are *Salix discolor* Muhl., *S. bebbiana* Sarg., and *S. pedicellaris* Pursh. This shrub zone is narrow, irregular, and in places poorly defined or absent. Although the herbaceous species are primarily those of the herb mat, *Menyanthes trifoliata* L. and *Potentilla palustris* (L.) Scop. reach their peak abundance in this shrub zone. We designated this community the "primary shrub zone" to distinguish it from the secondary shrub community occurring successionally and geographically after the tamarack forest.

Beyond the shrubs, and sparsely invading them, is a forest of tamarack with a much firmer peat substrate. Tamarack commonly occurs in pure stands with a shrub layer of *Ilex verticillata* (L.) A. Gray, *Rhus vernix,* and *Rhamnus frangula.* Although the arboreal aspect of the community is wholly tamarack in most portions of the forest, along the western margin tamaracks become mixed with *Betula purpusii* Schneid. or locally yield to *Betula lutea* Michx. f., *B. papyrifera* Marsh., or *Populus tremuloides.* Of the herbs present, *Osmunda cinnamonea* L. is of greatest importance with *Onoclea sensibilis, Trientalis borealis* Raf., and *Carex trisperma* Dewey as significant associates.

Outside the tamarack forest is the secondary shrub zone composed primarily of the three shrub species in the forest. Tamaracks gradually become less abundant in the transition from the forest to the shrub community, but in places the tamaracks abruptly give way to the secondary shrubs. *Betula lutea, Populus tremuloides,* and occasionally *Betula papyrifera* intervene in the transition in a few isolated areas along the northern boundary of the forest. Many dead tamaracks, both standing and fallen, are present in the secondary shrubs. Important herbs in the secondary shrub community include *Potentilla palustris, Onoclea sensibilis,* and *Osmunda cinnamomea.*

The bog is surrounded by a marsh, nearly absent in places, but generally moat-like, and expanding to occupy the southern quarter of the depression (Fig. 2). Principal species are *Phalaris arundinacea* L., *Solanum dulcamera* L., *Typha latifolia, Dryopteris thelypteris,* and *Poa palustris* L., with *Betula pumila* and *Spiraea alba* DuRoi of importance in the southern marsh near the shrub zone.

The transition between the shrub and marsh communities varies. Often it is abrupt, marked by a dense growth of unusually large *Ilex verticillata.* This winterberry thicket comprises an almost continuous zone around the bog. In a few areas, a totally distinct community intervenes between the dense winterberry growth and the marsh. The aspect of this community is a parkland of regularly scattered *Rhus vernix* shrubs and trees of unusually large size. The understory consists of *Sambucus canadensis* L., *Cornus obliqua* Raf., *Geum canadense* Jacq., *Urtica gracilis* Ait., *Smilacina stellata* (L.) Desf., *Lactuca biennis* (Moench) Fern., *Solidago gigantea* Ait., and other mesophytic species. The *Rhus* parkland usually is separated from the marsh by groves of *Populus tremuloides.* Associated with aspen in the groves are *Rhus vernix, Cornus obliqua, Ambrosia trifida* L. and *Arabis laevigata* (Muhl.) Poir. Both the aspen groves and the *Rhus* parkland contain species present in other bog communities, but there is a prevalence of mesophytic and wet mesophytic species as opposed to the more typical bog plants. The bog plants that do occur are those of apparently wide ecological amplitude. such as *Rhus vernix, Osmunda cinnamomea,* and *Onoclea sensibilis. Acer negundo* L. is widely scattered in these communities, increasing in frequency in the aspen groves.

Two separate and distinct tamarack forests are present in Volo Bog (Fig. 1). The northern forest is on woody peat and is separated from the southern forest, described above, by a shrub zone composed primarily of *Rhamnus frangula.* In a very restricted open area on the northern edge of the north forest, a surface layer of appressed, slow growing Sphagnum is present. A dense to scattered growth of *Chamaedaphne calyculata,* with less frequent *Vaccinium corymbosum* L. forms a shrub zone without noticeable herbaceous associates in this Sphagnum area. The tamarack forest, composed only of tamaracks with an understory of *Rhamnus,* is invading this shrub community. *Rhamnus* apparently has invaded and replaced much of the original community in the northern basin; it now forms an exclusive shrub community consisting only of very large, often tree-like shrubs and a few herbaceous species, especially *Dryopteris spinulosa* (O. F. Muell.) Watt. Waterman (1921) indicated the presence of other shrub species in this area, especially *Vaccinium corymbosum,* but *Rhamnus* was not mentioned in his papers. Ring counts of *Rhamnus* in this area indicate that many plants, at least, were present during Waterman's studies. Therefore, the possibility of misidentification on his part must be considered and the nature of the original community in this area is thus not known. This *Rhamnus* community corresponds with the limits of woody peat distribution, as apparently some former community once did.

Successional Processes

Classical hydrarch succession is clearly evident around the pool in the southern basin. The floating mat is advancing on the open water and, based upon photographs, has encroached perhaps one or two meters since Waterman's studies (1923). Waterman (1923, 1926) noted that the pool had occupied nearly all of the area surrounded by tamaracks as late as about 1870, and that the mat had invaded since that time.

This rapid development of the mat probably explains the distribution of *Chamaedaphne calyculata* around the pool. This species is almost totally restricted to one small heath-like area surrounded on three sides by tamarack. It otherwise occurs only as a narrow fringe along some portions of the tamarack forest. *Chamaedaphne* probably marks the extent of the mat before the period of rapid expansion. This shrub has been unable to invade the newly developed portions of the mat, which apparently remain unsuitable for the species for reasons not known to us. Other shrub species are invading the mat, judging from the distribution of individuals of the component species. Consequently, the primary shrub zone, except for the limited area described above, is not of the typical *Chamaedaphne* type generally described in the literature.

Regardless of the composition of the primary shrub zone, tamaracks obviously invade this community. Tamarack saplings occur in virtually all portions of the primary shrub zone, albeit infrequently, with the possible exception of areas of dense *Betula pumila*. With establishment of the tamarack forest, *Rhamnus* and *Ilex* appear. *Rhus* persists and increases in size (See Fig. 5).

With the decrease in density of the tamaracks with age of the forest, the subordinate shrubs became dominant and form the secondary shrub community (See Fig. 6). Since this community is the most extensive vegetation type in the bog, it is curious that earlier workers have failed to recognize it. Dachnowski (1912)

FIGURE 6.—Winter view of secondary shrub community from elevated position.

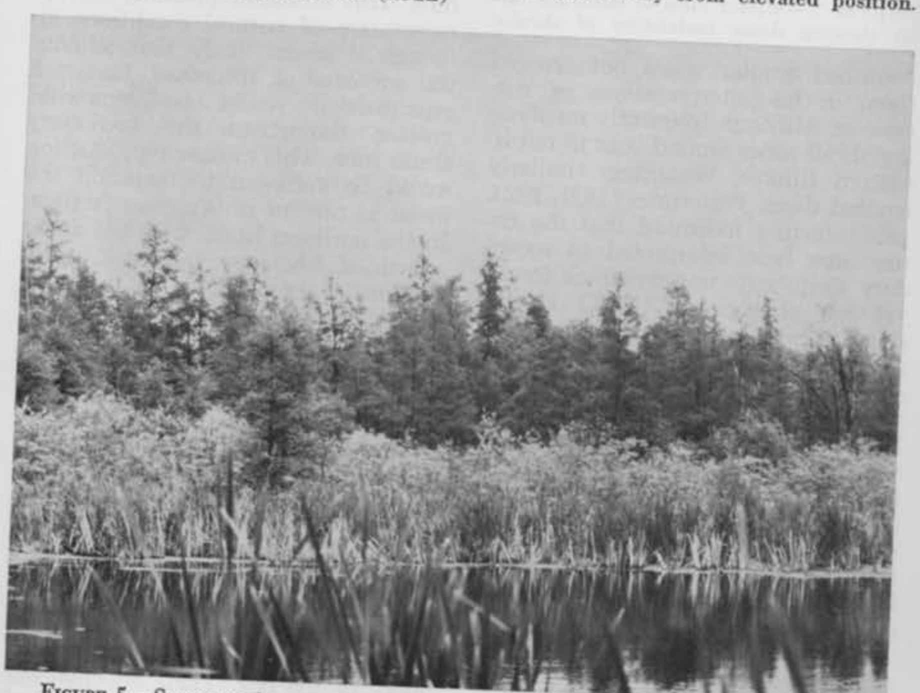

FIGURE 5.—Summer view across central pool showing herb mat, primary shrub zone and tamarack forest.

FIGURE 7.—Winter view of tamarack forest showing dense understory of shrubs.

described similar zones but ignored them in his interpretations of succession. Although frequently mentioning shrub zones around bogs in northeastern Illinois, Waterman similarly ignored them. Waterman (1921, 1923, 1926) further indicated that the entire area here interpreted as secondary shrub zone was tamarack forest, yet his photograph (1921) clearly shows a prominent shrub zone, much greater in extent than his term "border" implied. Kurz (1928) supplied a cross sectional diagram of Volo Bog also omitting this zone. The best description of the bog is provided by Reichle (1969), but he too ignored the secondary shrub zone and indicated a transition between the tamarack forest and the mesophytic forests of the uplands. We see little evidence for such a transition.

Transeau (1903, 1906) repeatedly emphasized that the bogs in southern Michigan and northern Indiana were in no way related to the surrounding oak-hickory forests, and that succession from bog mat to mesophytic forest did not occur. This is clearly the case at Volo and other nearby bogs, but apparently has been overlooked by other local workers. The dense growth of shrub species and *Osmunda cinnamomea* in the older portions of the tamarack forest (Fig. 7) preclude general reproduction of tamarack, and with the death of older trees the shrubs assume dominance. This process probably has been enhanced greatly by the invasion of *Rhamnus*. The presence of *Rhamnus* may explain, at least partially, the loss of the scattered tamaracks between the two present forests, although the actual cause of death of the older trees is not definitely discernable, as discussed later. In typical secondary shrub zone, as in the southern basin, tamaracks are very scattered and young trees are rare. This situation probably is representative of natural conditions although it seems likely that without the presence of *Rhamnus*, tamarack reproduction would be somewhat greater throughout the secondary shrub zone. This meager reproduction would be sufficient to maintain the forest as present in Waterman's time. In the northern basin, with the dense growth of *Rhamnus*, tamarack reproduction is absent. Even in the more natural secondary shrub zone of the southern basin, tamarack reproduction declines and eventually ceases as the shrubs mature and the community becomes more dense.

The invasion of *Rhamnus* raises the question of concurrent disturbance. As mentioned previously, the northern basin was cut over, and the associated vegetation has been replaced almost totally by *Rhamnus*. In addition to *Rhamnus* invasion, drainage may be a factor. Two drainage ditches are present on the periphery of the bog. Their effectiveness appears to be very local. The loss of tamaracks in the secondary shrubs of the northern basin and their decline in the southern basin evidently was abrupt, judged by the abundance of dead trees in approximately the same degree of decomposition. Perhaps the decline of the tamaracks in the shrub communities was influenced by drainage, although there is no evidence that the tamarack forest suffered much loss. Waterman (1926) believed a regional lowering of the water table was responsible for the general demise of the bogs in this area. The combined effects of moisture stress and the activity of bark beetles may have been responsible. Shelford (1963) reported heavy damage to the tamaracks of Volo Bog resulting from an outbreak of these insects about 1942, and many of the dead tamaracks exhibit bark beetle damage.

Although drainage, bark beetles, and invasion of *Rhamnus* may account for the loss of tamarack in the secondary shrub zone, the trees originally were very scattered and we do not consider the secondary shrub zone itself to be a product of disturbance. Undrained and little disturbed bogs in this area exhibit a similar shrub pattern.

Transeau (1905) described vegetation communities similar to the secondary shrubs but suggested that they always resulted from cutting of the tamaracks. Such was not the case at Volo Bog. Waterman (1921, 1923, 1926) reported that only the forest in the north end of the northern basin was cut. This area since has been repopulated by tamaracks. The evidence indicates that the secondary shrub zone at Volo Bog, and doubtless comparable zones in other bogs in this area, is a natural successional stage resulting from inhibition of tamarack reproduction through competition with the shrubs which become established in the tamarack forests. No direct succession from tamarack forest to mesophytic forest occurs. The presence of *Acer negundo, Populus tremuloides, Betula papyrifera, B. lutea,* and *B. purpusii* should not be construed as general mesophytic invasion as discussed later. A few individuals of *Acer saccarinum* L. were encountered in the bog and, although indicating that succession may eventually lead to mesophytic forest, they were so infrequent as to indicate no general invasion of mesophytic forest as occurs in the Northeast. The secondary shrub zone is a community of great stability, as stated by Transeau (1905), and appears to behave as a long-lasting subclimax. This is further emphasized by conditions in the northern end of the bog. Transeau (1905) stated that cutting or drainage of tamarack bogs may initiate wet-mesophytic invasion. Yet in Volo Bog, the cut-over northern portion of the bog, exhibiting a relatively drier woody peat, has grown back to bog vegetation. The *Rhamnus* forest, although an unnatural bog community, invaded long after the initial disturbance and must have eliminated another bog community. Mesophytic invasion had not occurred at the time of *Rhamnus* establishment, nor has mesophytic invasion yet occurred. The northern end of the bog, under conditions most favorable for mesophytic invasion, supports only a few widely scattered *Prunus serotina* Ehrh. and *Quercus rubra* L., usually growing near the border of the marsh.

Some quaking aspen occurs as scattered trees and one grove in the secondary shrub zone between the southern tamarack forest and the *Rhamnus* forest in the north (Fig. 1). Major development of the species is in scattered groves between the bog and marsh communities (See Fig. 8). According to Dachnowski (1912), quaking aspen in Ohio bogs is confined to areas of shallow or mineral-rich peat, a conclusion sup-

FIGURE 8.—Autumnal view of aspen grove from adjacent *Rhus* parkland.

ported by the high pH (averaging 5.9) of aspen soils at Volo. This is in sharp contrast to the tamarack and secondary shrub communities, where soils range from pH 3.1 to 4.9. This explains the peripheral locations of the groves and also the east-west extension of scattered trees between the southern tamarack forest and northern *Rhamnus*-dominated shrub zone. The location of groves on the periphery of the bog communities and immediately adjacent to the marsh reflects proximity to the calcareous, base-rich till of the uplands and drainage derived from it. Artist (1936) indicated a till ridge extending to within less than two meters of the surface of the bog in the general area of east-west aspen extension. This ridge evidently supplies sufficient mineral infusion of the peat to support the aspen. Therefore, it appears that quaking aspen bears no direct successional relationship to the other bog vegetation but rather occurs in response to local edaphic conditions.

The distribution of *Betula lutea*, *B. papyrifera*, and *B. purpusii* appears to be similarly based. All occur in the region of east-west aspen extension. *Betula purpusii* reflects its hybrid ancestry ((*B. lutea* x *B. pumila*) by ranging rather widely from this area, with one plant in the primary shrub zone, although the behavior of the hybrid is most like that of *B. lutea*.

The *Rhus* parkland (Fig. 9) has a consistent relationship to the aspen groves, always occurring between the aspen and the secondary shrub zone. A zone of unusually large *Ilex* separates the secondary shrub zone from the *Rhus* parklands. The significance of these parklands is obscure. They may represent, like the aspen groves, a segregation of species in response to local edaphic conditions, as is indicated by the pH of parkland soils (averaging 5.8). Aspens appear to invade only rarely the periphery of the parklands. The herbaceous and shrub synusia of both the parkland and aspen groves are quite distinct, although both are markedly mesophytic. Along the western margin of the southern tamarack forest, in an area of compressed zonation, an embryonic *Rhus* parkland occurs in the mature tamarack forest. The adjacent secondary shrub zone supports scattered aspen. This parkland is clearly originating within the tamarack forest although it may not be a component of the forest, but rather an independdent community formed at the time of primary shrub and tamarack invasion. The adjacent aspen grove, however, is invading the secondary shrub zone. Thus these two vegetation types may originate under different successional regimes, resulting in different floras. This also explains the lack of aspen invasion of the *Rhus* parkland; they are not successionally

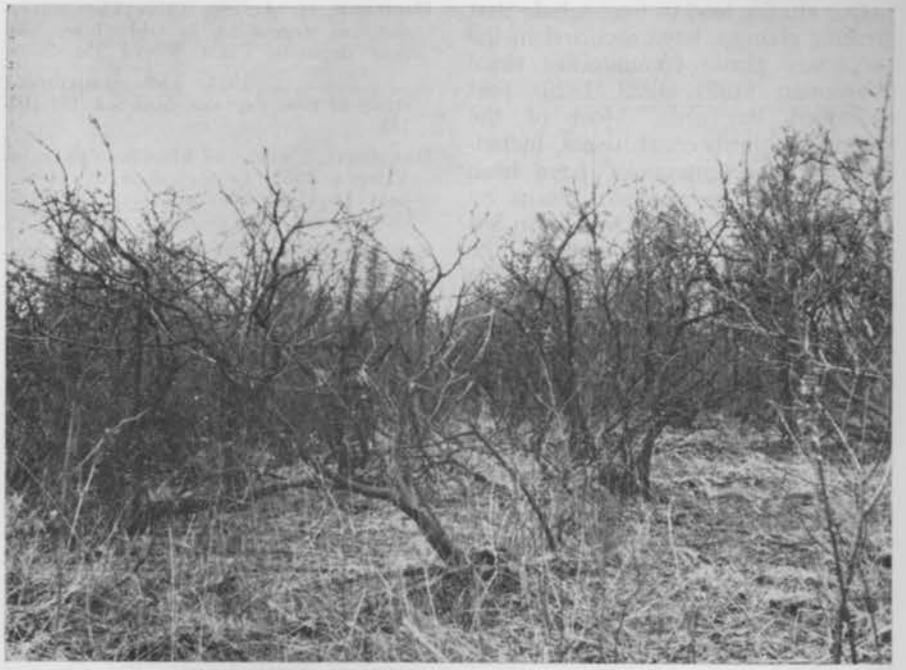

FIGURE 9.—Autumnal view of *Rhus* parkland with typical, widely spaced, large poison sumacs.

related. It appears that the *Rhus* and aspen vegetation manifest different responses along an edaphic gradient, probably reflected by base saturation of the peat.

The *Rhus* parkland and aspen groves exhibit evidence of succession toward more mesophytic species. This especially is evident with *Acer negundo* invasion. Many dead aspen and *Rhus* are present in these communities but vegetative reproduction is continuing under the very open canopies. It is difficult to estimate how persistent these communities will be, but the sharp transition between secondary shrub communities and the *Rhus* parkland suggests a very stable relationship.

CONCLUSIONS

Vegetation of Volo Bog, generally considered to represent classical hydrarch bog succession, was intensively studied. Two basins are easily discernable from the vegetation patterns. Primary attention is given to the southern basin which most clearly exhibits the successional processes. Vegetation was classified into five primary types in roughly concentric zones around the open pool and two minor vegetation types scattered irregularly between the two outer zones. The pool is surrounded by an herb mat, giving way irregularly to a primary shrub community that is invaded by a tamarack forest. The tamarack forest is replaced by a long-persisting secondary shrub community. Girdling the secondary shrub vegetation is a marsh. The secondary shrub-marsh ecotone is irregularly interrupted by development on more mineralized peat of the minor *Rhus* parkland and quaking aspen vegetation types.

Our studies lead us to conclude that striking changes have occurred in the secondary shrub communities since Waterman (1921, 1923, 1926) first described the area. Most of the secondary shrub constituents, including scattered tamaracks, have been replaced in the northern basin by *Rhamnus frangula*. *Rhamnus* also has become a dominant species in the secondary shrub community in the southern basin and in tamarack forests and may be hastening the replacement of tamarack by shrub species. Demise of tamarack also may have been influenced by lowering of the watertable and a bark-beetle outbreak.

No evidence could be found for succession leading to mesophytic forest, except on small areas of mineral-rich peat. With exception of the *Rhamnus* invasion, the secondary shrub community appeared to be stable with shrub species reproducing throughout.

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