Distribution patterns of mudflat vegetation in Iowa flood control reservoirs

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Distribution patterns of mudflat vegetation
in Iowa flood control reservoirs

by

James Henry Wilson

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Department: Botany and Plant Pathology
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Ames, Iowa

1973
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INTRODUCTION

How charming the contrast of land and water, especially a temporary island in the flood, with its new and tender shores of waving outline, so withdrawn yet habitable, above all if it rises into a hill high above the water and contrasting with it the more, and if that hill is wooded, suggesting wildness! Our vernal lakes have a beauty to my mind which they would not possess if they were more permanent. Everything is in rapid flux here, suggesting that nature is alive to her extremities and superficies.

--Henry David Thoreau

The above sentiments (Torrey, 1906) were expressed nearly a century before the construction of the large flood control reservoirs of Iowa referred to in this study. The low, frequently inundated areas of these reservoir basins bear little resemblance to pristine wilderness. Yet these vast tracts of public land have a character—a harsh wildness, a stark surrealism—that is equaled by few Iowa landscapes.

Flood control reservoirs are characterized by fluctuating water levels. By design, these reservoirs store flood waters during times of high run-off and release these stored waters gradually to the parent stream. Thus a more stable water level is achieved below the dam at the expense of frequent and often extreme water level fluctuations in the impoundment. The nature of this area of fluctuation, called the flood control or flood pool, varies from terrestrial to aquatic and back again. Furthermore, the timing of each flood period is not predictable in advance of the weather patterns which cause the flooding. The upper reaches of the flood control pool may be flooded so infrequently as to
allow the basin to be used for agricultural purposes. The lower portions, however, may be subject to inundation several times per year. This low, often inundated ground is characterized by willow thickets and weedy herbaceous growth. Such land areas of gentle slope, partially or completely exposed during the conservation pool level and covered when this level is exceeded by a rise of several feet, have been described by Tiemeier (1951) as mudflats.

These vast expanses of bare mud, weeds and shrub thicket are not well accepted by the public (Committee on Allerton Park, 1971). This esthetic liability is most apparent when crossed by a major highway as is the case at Red Rock Reservoir in Marion County, Iowa. This aspect has taken on added significance in the past few years with the increasing environmental awareness of the public and the passing of the National Environmental Protection Act of 1969. The task has largely fallen to biologists to define, predict and suggest management schemes for these immense by-products of flood control projects. Unfortunately, relatively little information is available on which to base such guidelines.

These mudflat areas are not easily defined; certainly they are not always muddy nor completely flat. While silt deposition occurs over much of such an area, siltation is not necessary to the mudflat aspect. It is tempting to define mudflats as the area of the flood pool below the elevation of predicted x-year flood frequency, with the x-year being defined as 10 or less. Such a definition would give distinct boundaries to the defined mudflats, but may not be realistic for other reasons. First of all, since the mudflat aspect develops very rapidly, a prolonged
abnormally large flood or a sequence of abnormal floods could generate this aspect on any gently sloping land areas within the flood pool. This fact alone argues for the designation of all gently sloping areas of the flood pool as "potential mudflat." Furthermore, predictions of flood pool levels are based on river flow data from past records. There is no reason to assume that the frequency of past maximum flood levels will not be repeated or exceeded in the future. The prevailing aspect of any contour level is not, then, a simple function of flooding frequency, but is dependent upon the extent of disturbance caused by each flood and the rate at which the vegetation recovers from that disturbance as compared to frequency of flooding.

If this low, often inundated ground is to be circumscribed in terms meaningful to description and management, sooner or later it becomes necessary to define the area in terms of vegetation. This, too, has inherent problems. In established Iowa reservoirs, the upper limits of the mudflat area might be defined by the presence of the Salicetum (Conard, 1952), the woody community dominated by willows and soft maples. If a reservoir has been completely filled for a period of time, however, this type of community may be found at the upper limit of the flood pool. Such a situation would hardly justify designating the entire pool as mudflat.

Recognizing these problems, it may be advisable to skirt the issue of definition and simply describe characteristics which typically occur in Iowa reservoir mudflats. In general, mudflats commonly occur on, but may not be restricted to, the gently sloping areas of the active flood
pool and substrates exposed by lowering of the permanent pool level (Fig. 1). Mudflat substrates (often called soils in this study) tend to be alluvial material with a relatively high water table. Colonization in early stages is by *Salix*, *Populus* and *Acer* seedlings and weedy annual herbaceous species. Older reservoirs may support biennial and perennial semiaquatic to terrestrial herbaceous species. Woody species tend to proliferate to the thicket stage.

Iowa flood control reservoir mudflat vegetation often occurs in striking zonation patterns which appear to approximate contours about the flood pool (Fig. 2). Such patterns are common in nature and have been reported in various riparian situations including river (Lindsey, Petty, Sterling and Asdall, 1961), lake (Reed, 1902; Graham and Henry, 1933; Raup, 1935; Mandossian and McIntosh, 1960), and marsh (Cottam and Bourn, 1952). It is understood that these zones are expressions of local conditions and reflect differences of important factors of the habitat (Braun-Blaunquet, 1932). While these factors have been the subject of discussion (Kershaw, 1963) quantitative data have been largely lacking.

Studies of the vegetation affected by fluctuating water levels have been largely confined to wetlands utilized by waterfowl and other wildlife. General observations on plant communities (usually reported on the basis of one or two dominant species), as they relate to waterfowl habitat, are abundant in the literature (Uhler, 1944; Newson, 1967; Sanderson and Bellrose, 1969; Bennett, 1971). Adequate information is not available for vegetation management on lakes in the upper Midwest with extreme
Fig. 1a. Diagrammatic top view of a flood control reservoir showing the location of potential mudflats in relation to the conservation and flood control pool.

Fig. 1b. Diagrammatic cross section of a flood control reservoir showing the elevation of potential mudflats in relation to that of the conservation and flood control pool.
Fig. 2. Photograph of zonation on area 1-2, east of highway 14 bridge, September 11, 1971
water level fluctuation. Recognizing the need for descriptive information on Iowa reservoir mudflat vegetation, this study was initiated with the following objectives in mind:

1) To document observed vegetation patterns in well located study areas on reservoir mudflats.

2) To investigate the relationship of these observed patterns to the distribution of individual species.

3) To investigate and attempt to characterize possible environmental gradients associated with these patterns.

4) To examine the results of the above observations with respect to plant succession and possible reservoir management techniques.
DESCRIPTION OF RESEARCH AREAS

Observations have been made at two flood control reservoir sites in Iowa (Fig. 3). The mudflats of the Red Rock Reservoir, on the Des Moines River in south-central Iowa, were chosen for intensive study. Since pattern in plant communities often is most distinct in immature vegetation (Kershaw, 1963), Lake Red Rock, having filled for the first time in 1969, was a logical place to observe discrete vegetation zonation. Coralville Reservoir, on the Iowa River in east-central Iowa, was initially filled in 1958. The vegetation of the mudflats associated with this reservoir was included in the present study because of the age of the reservoir and the slightly different operational scheme involved.

These reservoir areas have a moderate climate. Annual mean temperatures for the Red Rock and Coralville areas are 51°F (10.6°C) and 50°F (10.0°C), respectively. Annual mean precipitation averages 32 inches in both areas, with an average of 22 inches occurring in the April through September period. Monthly precipitation averages are highest in spring and early summer (Shaw and Waite, 1964).

Landforms in the Red Rock Reservoir area are characterized by the wide, flat flood plain of the Des Moines River and moderately steep to steep valley slopes. In a few places, eroded sandstone outcroppings

---

1Description of the physical features and management schemes of the Red Rock and Coralville Reservoirs is based on information provided by and used with the permission of the U.S. Army Corps of Engineers, Rock Island District, Rock Island, Illinois.
Fig. 3. Vicinity map showing the flood control reservoir system proposed for Iowa. This study is concerned with aspects of the Red Rock and Coralville Reservoirs, with Red Rock receiving the more intensive examination.
VICINITY MAP

SCALE IN MILES

SIOUX CITY
COUNCIL BLUFFS
RED ROCK RESERVOIR
DUBUQUE
BACON RIVER
RACCOON RIVER
DES MOINES
CEDAR RIVER
CEDAR RAPIDS
DES MOINES
SAYLORVILLE RESERVOIR
CORALVILLE RESERVOIR
WAPELLO
ROCK ISLAND
KEOKUK
MISSOURI
CHARTON RIVER
M. MISSOURI
WASHINGTON RIVER
IOWA CITY
DAVENPORT
ROCK RIVER
D. MISSOURI
WISCONSIN RIVER
S. DAKOTA
MISSISSIPPI RIVER
KANSAS
QUINCY
SCALE IN MILES

MINNESOTA
WISCONSIN
WIS.

IOWA
COUNCIL BLUFFS
RED ROCK RESERVOIR
RATHBUN RESERVOIR

SCALE IN MILES

VICINITY MAP
form nearly vertical valley walls. Uplands of the area are typically flat to rolling, formed of glacial till overlain with loess of varying thickness.

At an elevation of 725 feet above mean sea level, the permanent pool of Red Rock Reservoir has an estimated surface area of 8,950 acres and extends 11.3 miles upstream. At the full flood pool elevation of 780 feet, the lake surface area is approximately 65,500 acres, extending 33.5 miles upstream. The land surface area subject to inundation with extreme flooding may then be estimated at more than 56,500 acres.

The irregular shoreline of the Coralville Reservoir conservation pool rises abruptly from the Iowa River floodplain to the upland. Slopes of the flood basin vary from gentle to steep. At an elevation of 680 feet above mean sea level, the permanent pool of approximately 4,900 surface acres has a length of about 22 miles. The flood pool has a surface area of approximately 24,800 acres at an elevation of 712 feet and a length of 35 miles. Pertinent physical data on these two reservoirs are presented in Appendix A.

Operation of the Red Rock Reservoir consists of storing the excess flood waters of the Des Moines River and releasing these waters as the river level permits. Operation of the Coralville Reservoir is somewhat more complex, with the conservation pool being held at an elevation of 670 feet in the spring for maximum flood control and 680 in the summer when flooding is less probable. In autumn, the permanent pool level is permitted to rise to 683 feet to accommodate waterfowl management on the area. The pool level is returned to the 680 elevation in winter.
Details of these operational plans are presented in Appendix B.

While limnological inquiry is not within the scope of this project, some indication of the quality of the surrounding water should be included in the description of mudflat areas. Water grab samples were taken at three points near the conservation pool level (Fig. 4) over a 24 hour period, August 19-20, 1971. These samples were analyzed in the field for temperature, pH, dissolved oxygen, phenolphthalein alkalinity and total alkalinity, using published methods (Hach, 1967).

Temperature variations during this 24 hour period ranged from 22-31°C. The pH values encountered varied from 7.5-8.5. Dissolved oxygen concentrations reached a high of 5.6 ppm and dropped as low as 1.3 ppm. Phenolphthalein alkalinity was, of course, undetectable at pH values below about 8.3, but rose as high as 20 ppm expressed as calcium carbonate. Total alkalinity varied from 202 to 220 ppm expressed as calcium carbonate. These data are reported as diurnal curves in Appendix C.

The Red Rock Reservoir lies within the Clinton-Keswick-Lindley soil association area of Iowa. Soils of the flood control pool have been described by the U.S.D.A. Soil Conservation Service of Knoxville, Iowa. The approximate distribution of soils in the Red Rock flood pool is shown in Fig. 5. The mapping of these soils by the Soil Conservation Service is quite general; soils are often separated on the basis of vegetation types. The major soils of the flood control pool are described in Appendix D.

Soil temperatures were found to vary considerably with the
Fig. 4. Map showing sampling stations a, b, and c from which water surface grab samples were taken hourly, August 19-20, 1971.
Fig. 5. U.S.D.A. Soil Conservation Service soil map of the Red Rock Reservoir flood pool, soil descriptions are found in Appendix D.

legend:

88  Nevin silty clay loam
133  Colo silty clay loam
220  Nodaway silt loam
315  Alluvial land
354  Marsh
467  Radford silt loam
485  Spillville loam
vegetation. The effect of vegetation on soil temperature as well as variation of soil temperature throughout the day is shown in Fig. 6. Continuous soil temperature data are not available for the mudflat area, but U.S. Geological Survey air temperature data are available from Knoxville, Iowa, about 5 miles south of the mudflat area. Soil temperatures, from 4 inches below the surface, are available from Ames, Iowa. These data are summarized in Appendix E.
Fig. 6. Soil surface temperature fluctuations on bare mudflat and an adjacent zone of *Bidens* spp., September 11, 1971
Meaningful vegetation study on Iowa flood control reservoir mudflats often involves a compromise between the ideal and the practical. One of the first such compromises involves the intensity of study attempted. The amount of land involved, approximately 75,000 acres of the reservoirs in this study, precludes sampling a large percentage of the area with great precision. Furthermore, the nature of a reservoir flood pool limits the number of sampling sites to which easy access can be obtained. These limitations must be reconciled with the need for as much specific information as possible. In transect studies of vegetation pattern, relatively small plots must be examined, since pattern cannot be readily detected on a scale smaller than the plot size employed. In order to detect small scale changes in pattern, it is obviously desirable to keep sample plots as close together as possible. This minimizes the possibility of the sampling scheme skipping a very small vegetational unit, but the technique may be frustrated by sharp physical breaks in the continuity of the study area.

This study of mudflat vegetation incorporates general observations and descriptions in areas of limited access and very specific vegetational data in well defined intensive study areas. Vegetation studies were initiated during the 1970 growing season and continued through autumn, 1971, at both reservoir sites. During this time, frequent trips were made to Red Rock Reservoir, averaging more than one per week as conditions permitted, during the growing season. Repeated observations
were made and documentary photos were taken at established stations throughout the flood pool. Twice during each growing season, aerial survey flights were made. Oblique documentary photos were made using 35 mm black and white, color and false color near-infrared film, to be used in correlating observations.

With the advice and assistance of Mr. John Beamer, manager of the wildlife refuge in the Red Rock flood pool, periodic access by foot, car and boat was gained to less accessible areas of the upper reaches of the flood pool. While many of these observations were qualitative and not repeated, they were useful in providing an understanding of the total flood pool vegetation.

Descriptions of apparent species groupings were included across the topographic gradients of the flood basins, and indications of the history of use of the area were recorded. Observations attempting to relate species to their relative topographic position both near the conservation pool level and in the upper reaches of the reservoirs were made where reasonable access was possible.

Observations at Coralville Reservoir were less extensive. General information, as described above for Red Rock, was recorded at several relocatable stations within the Coralville flood pool. Plant collections and documentary photos were made at each station. This information was used to compare communities of the two reservoir mudflat areas with respect to species occurrence and zonation pattern. Field collections of mudflat plant species, made throughout the 1970 and 1971 growing seasons, were used to confirm identification of recognizable
taxonomic units. Taxonomy of semiaquatic plant species follows Fawcett (1957); terrestrial species follow Gleason and Cronquist (1963); grasses follow Hitchcock (1950).

It was decided to establish intensive study areas in the most active part of the flood pool at Red Rock; that is, the area of the flood pool nearest the level of the conservation pool and, therefore, the part of the flood pool most likely to be influenced by any rise in water level. Since sharp physical or topographic breaks are not prohibitive in the area, continuous transects were established across zonal patterns in area I-1 and I-2 (Fig. 7).

Area I-1, at the very junction of the permanent and flood pools, is an island. Four parallel transects crossing this island in a north-south direction intersect the topographic contours as well as the zones of vegetation of the island. These transects provide a comparison of north and south facing slope aspects within a relatively short distance.

Transects in area I-2 extend to a higher topographic position and are considerably longer than those of area I-1. Consequently, this area is less affected by small changes in reservoir water level than is area I-1. Parallel transects across the gradual slope of area I-2 intersect several apparent zones of vegetation between the 736 foot elevation and a small pool whose water level fluctuates with that of the main body of the reservoir. An incidental but attractive feature of area I-2 is its proximity to the large bridge on highway 14, spanning the Des Moines River and the mudflat expanse. This bridge provides an elevated and easily accessible observation and photo station for the I-2 study area.
Fig. 7. Map of Red Rock Reservoir flood control pool showing location of intensive study areas I-1 and I-2, and experimental planting sites P-1 and P-2
Red Rock Twp. v Union Twp.
and the surrounding mudflat vegetation.

Topographic Description

Topographic relief was defined by shooting relative elevations at five meter intervals along each of the four parallel transects of area I-1. An alidade, plane table and stadia rod were used in the standard manner as described by Low (1952). These elevations were related to the water level, for which daily absolute elevation is recorded by the U.S. Army Corps of Engineers. A similar procedure was used to establish elevations at twenty-five meter intervals along transect I-2.1.

Collection and Treatment of Transect Data

The phenology of plant species within an area of fluctuating water level is often chronologically behind the phenology of the same species outside the fluctuation zone (Penfound, Hall and Hess, 1945). This delay in the onset of maturation and flowering makes identification of many species impossible before mid-August. This time factor and the need for a large number of samples led to the collection of presence-absence data and subjective assessment of species dominance along established transects in areas I-1 and I-2. All transects were examined during the third and fourth week of August, 1971. Presence data were collected for all identifiable taxa rooted in contiguous square meter plots along each transect line. The collection of such data is not only much faster than more quantitative measures, but these data give an adequate
indication of species distributions within the area and are easily applicable to several types of numerical analysis.

A number of numerical techniques are available for use in vegetation description; the choice depends to a considerable extent on the objective of that description. In this study, it was desirable to objectively delimit the boundaries of recognizable zones within the vegetation pattern. After these boundaries were precisely described, environmental data could be related to the discrete area of the zone.

Two general types of procedures have been used in the numerical description of vegetational transect data. One of these types, ordination, is a popular group of techniques which represent vegetational units on a relative scale. While ordination techniques may yield useful information concerning relationships between units of vegetation, groupings of these units are not discrete. The absence of well defined vegetational groups make ordination techniques inappropriate for studies of strong pattern in vegetation (Goodall, 1970; Kershaw, 1964).

A second group of numerical descriptive procedures are called classification techniques. The various procedures of this type result in discrete, if somewhat arbitrary, groupings of the units examined. A classification technique, then, will objectively group plots of a transect, without regard to the subjectively determined pattern of the plots.

Several types of classification techniques are available for use in vegetation description. Cluster analysis is a general term given to a large class of popular numerical techniques for defining groups of
related units based on similarity coefficients. While the possible variation in clustering techniques is multitudinous, the variation in results is of a lesser magnitude.

In general, such analyses are of two forms. "R"-analysis treats individual species as individuals of the population to be clustered. In the clustering procedure, the occurrence of each species in the various plots is treated as an attribute of the species. "Q"-analysis, conversely, treats each plot as an individual to be clustered. The species occurring in each plot become characteristics of that individual plot.

Cluster analysis techniques have been used to characterize ecological associations. For example, vegetation data from a series of plots forming a transect across a shallow lake were clustered on single linkages of similarity coefficients. This technique brought together quadrats from reed swamp, fen, and carr (swampy willow thickets) associations which bordered the lake. These differentiations were generally like those made from other classification techniques (Sokal and Sneath, 1963).

In this study, vegetation data from contiguous square meter segments of the transects of areas I-1 and I-2 were clustered using the unweighted pair-group method (McCammon and Wenninger, 1970). Data from each transect were clustered separately. Simply stated, this procedure initially treated each square meter as a separate group. A similarity matrix was computed for all groups in each transect. During each clustering cycle, the most similar pair-groups were joined to form a
new group. The hierarchical arrangement which resulted was expressed as a two-dimensional diagram, called a dendrograph (McCannmon, 1968). A clustering level was then chosen which gave a plot grouping corresponding, more or less, to the subjectively determined pattern.

Soil Analysis

Soil samples were collected from the top 5.0 cm of mineral soil at 10-meter intervals along transects I-1.1 and I-1.3. Additional samples were taken at 5-meter intervals near the ends of the transects where vegetation zonation appeared most intense. Similar collections were made at 25-meter intervals along transect I-2.1, with additional samples taken where vegetational or topographic change was abrupt.

Percentage moisture content was gravimetrically determined at each soil sampling site by the following method. Soil samples were collected in soil cans, sealed and weighed in the field to the nearest 0.1 gram. These cans were later unsealed, placed in an oven at 100°C for 48 hours, cooled and reweighed. Both weights were corrected for weight of the cleaned, oven-dried can. The net difference in weight of the soil was taken as the weight of water in the soil sample and used to calculate percent moisture in the original sample.

Air-dried soil subsamples were sent to the Soil Testing Laboratory, University of Wisconsin, Madison, Wisconsin, for the determination of available NO₃-N, P, K, pH and conductivity by methods on file there.

Texture analysis of duplicate soil subsamples was accomplished by the standard pipette analysis (Troeh and Palmer, 1966). This procedure,
based on a difference in settling rates of different sized particles, separated mineral soil samples into the following particle size categories:

- sand .05-2.0 mm
- large silt .02-.05 mm
- fine silt .002-.02 mm
- clay less than .002 mm

Agreement within 2 percent in each size category, on duplicate samples, was considered to be the limit of precision of the method.

Percent organic matter in soil samples was approximated by the dry combustion of soil subsamples in a Thermoclyne muffle furnace. This procedure gives values which agree closely with the ash determination of oxygen bomb calorimetry (Reiners and Reiners, 1972). The problems associated with using the weight of material lost during combustion as total organic matter are discussed by Black (1968). While the errors introduced by these problems are probably not significant in the present study, results will be presented as percent loss on ignition. These values are probably an adequate reflection of organic matter in the range of precision reported. Weighed subsamples of approximately 10 grams of oven-dried soil from each sampling point along transects I-1.1 and I-2.1 were placed in the furnace for 12 hours at 500°C, cooled and reweighed. Samples were run in duplicate; all weights were read to four decimal places. Average values of weight loss are reported for each sampling point.
Experimental Planting

In conjunction with this study, experimental plantings were made in areas P-1 and P-2 (Fig. 7), adjacent to small, sometimes distinct, pools which fluctuate with the water table of the mudflats. Propagules of various wetland species were acquired from Wildlife Nurseries, Oshkosh, Wisconsin, and sown on wet mud by hand. Results were generally negative and will be specified in a later section.
RESULTS AND DISCUSSION

Occurrence of Pattern in Vegetation

Pattern in vegetation has been defined as the spatial arrangement of individuals of a species (Kershaw, 1964). The dispersion of propagules, local modification of the ecotope by older and contemporary plants of the same and other species, patterned variation in the ecotope, and large scale environmental variation may all contribute to the control of pattern in plant occurrence. Since any environmental variable may be associated with an undetected variable or variable complex, the ascription of vegetation pattern to any specific cause must be, to some extent, hedged with reservation. Even attempts to precisely define such relationships under controlled conditions may be unsuccessful, since the response of a species to any given variable may only occur with competition (Goodall, 1970).

Pattern in a single species has been classified as three types--environmental, sociological and morphological. Environmental pattern is often related to the response of vegetation to microtopographical, microclimatic and edaphic factors. Sociological pattern results from the interaction of two or more species such that the distributions of their populations exhibit a pattern which may or may not be related to environmental factors. Pattern of the above types is often readily observable in the field. A less obvious type of pattern is that caused by the morphology of a species. This morphological pattern is dependent on the sexual and asexual reproductive potentials of the species
and the population considered (Shimwell, 1971).

Within a hypothetical single species population in a uniform environment, the distribution of an individual in soil and air space is said to be radially symmetrical. Its vertical distribution is characteristic of the species as modified by competition and the environment. If conditions of the ecotope are stable enough relative to generation time for a steady state to be achieved, pattern in the vegetation will be uniform with random variation (Goodall, 1970).

In such a hypothetical uniform environment, a population of only one species is subject to at least two sources of pattern. The spatial relationship of seedlings to the parent plant may impose a pattern on distribution of the species by determining the area where offspring may become established. This establishment will, in turn, affect the distribution of successive generations. In communities of biennial and perennial species, this parent-offspring relationship may exert considerable influence on the observable pattern. In annual communities, where one generation is dead before the next develops, this effect may not be obviously manifested in the vegetation pattern. When seeds are widely scattered, this effect is lessened even more. In a flood control reservoir system, flood waters may distribute seeds hundreds of yards or even miles from their point of origin, although this is not necessarily the case. Seeds may be buried by siltation, only to be uncovered by localized erosion several seasons after the parent plant has died. The cracking of drying mud may also allow buried seeds to germinate and grow. Such characteristic disturbances make the effect of the
parent-offspring spatial relationship relatively unimportant in the
determination of mudflat vegetation pattern.

Another source of pattern in a single species population in a hypo-
thesically uniform environment is the group of relationships, exclusive
of parent-offspring relationships, between individuals of the same
species. These are included in the phenomenon called "sociological
pattern", and may include modification of the ecotope on the microenvi-
ronmental scale, the competitive advantage of given individuals, age
structure of the population and the effects of substances exuded by some
plants (Kershaw, 1964).

Nonrandomness in vegetation may also be produced by interspecific
competition. A dominant species which exhibits a pattern may impose a
counter pattern on a subordinate species. Even if the dominant species
exhibits random distribution, the pattern of an accompanying species
may be affected if the two species are positively or negatively corre-
lated (Goodall, 1970).

When several species tend to be found in constant association
through a mutual dependence on certain environmental characteristics,
these species have been said to compose an "ecological group." While
environmental requirements of such groups may overlap, any given group
will be found to exist only within a relatively narrow range of condi-
tions (Goodall, 1970). This concept appears to be useful in any con-
sideration of the status of vegetation zones on reservoir mudflats.
While it has not been shown that these zones are uniquely associated
with environmental discontinuities, observations indicate a close
association between zonation and conditions of exposure.

Vegetation patterns on low, often inundated ground have not been described in an extensive or consistent manner. Zones of dominance at the margins of various aquatic systems are easily observed and frequently reported in a qualitative and very general way. One such analysis of the mudflat vegetation of a flood control reservoir in Kansas (Tiemeier, 1951) described the area in terms of the five predominant genera with an estimate of the area dominated by each. In that reservoir at the time of examination, Polygonum dominated 310 acres, Helianthus and Xanthium codominated 199 acres, Erigeron was dominant on 110 acres and Chenopodium was dominant on 88 acres. Species names were not reported and vegetation description was not extensive since the work was primarily of a limnological nature; however, the paper does exemplify the frustrating lack of good information available for the mudflat habitat.

The vegetation immediately invading a drained impoundment in Massachusetts has been described (Robinton and Burk, 1972). Four distinct zones of vegetation were distinguished proceeding up an elevational gradient from the most recently exposed sediments. Successively higher zones of vegetation were assumed to represent progressively older vegetation which became established as the dam of the impoundment gradually failed. Certain species, including Mollugo verticillata and Chenopodium sp., were found only in later stages of vegetation development. Still other species, notably Leersia oryzoides, were found in all zones. Ambrosia, Bidens, Eupatorium and Impatiens achieved aspect dominance in
A description which could have established a logical procedure for future studies was reported by Hess and Hall (1944). Contour zonation of vegetation in a flood control reservoir with a "normal" schedule of water level management was based on life forms found at the end of the growing season within the area of water level fluctuation. The upper part of the area subjected to inundation was characterized by "leafy erect terrestrial" species such as goldenrod (Solidago) and aster (Aster). Immediately downhill was a zone of "flexuous wetland species." "Agrostiform grasses" dominated the upper part of this zone while smartweeds (Polygonum) were predominant in the lower part. A band of "naked erect wetland species" was sometimes found in the lower part of the above zone. Spikerush (Eleocharis) was the typical dominant of such a vegetation band. Immediately above the lower limit of water recession was a zone of "wetland carpet species", typically tealgrass (Eragrostis) and water purslane (Ludwigia). While a particular life form might predominate in a particular zone, other forms were usually present and even became dominant within localized areas of the zone. In general, the following progression of plant forms was found from high ground to the reservoir proper: "woods, coppice, leafy erect, flexuous, naked erect, carpet, floating mat, submerged, pleuston."

Five zones of vegetation have been described in the lake basin of flood control projects in Oklahoma (Penfound, 1953). Very little zonation or vegetation development was considered possible in lakes with extreme water level fluctuation; the critical amplitude of fluctuation,
however, was not suggested. Usual zones are summarized as follows:

1) the drift line communities of varied species composition often including *Verbena* spp.

2) flood zone communities of two types including residual communities of native grasses and flood induced communities of varied species composition

3) a summer pool level of wetland plants often including *Carex*, *Cyperus* and *Panicum* species

4) a recession zone of variable character but consisting of emergent aquatics when soil is aerated for less than one month in summer; seepage areas of this zone typically supporting pure stands of *Leersia oryzoides*

5) a continuous water zone of floating leaf and submerged aquatic vegetation.

It has been suggested that the flood induced communities mentioned above are probably several different communities which have been treated as one. Variations of the above zonal pattern were frequently encountered.

In these Oklahoma flood control reservoirs, amplitude of water level fluctuation was thought to be the most critical factor in the establishment of vegetation. Extreme water level fluctuation prevented the development of the wetland fringe vegetation. Summer recession zones were not expected in reservoirs where extensive summer drawdown did not occur. Furthermore, extended periods of drawdown could make possible an inverted zonation by allowing terrestrial species to become established below their usual level (Penfound, 1953).
Vegetation of river floodplains, with a longer history of observation than that of flood control reservoirs, has had no better descriptions. In two river floodplains of Indiana, Lindsay et al. (1961) described riparian zonation beginning with the aquatic community. Eight zones were identified as follows:

1. aquatic zone; submerged and floating aquatic plants
2. zone of emergence; emergent aquatics, sedges, grasses and/or
   2a. a bar zone; resulting from temporarily receding water levels; essentially bare
3. annual grass-sedge-forb zone
4. perennial forb zone
5. marginal small tree zone
6. marginal tall tree zone
7. floodplain forest.

The soil-water relationship was felt to be the primary controlling factor in the striking zonation of these floodplains. These zones related to the average elevation of the various species above the average water level. Theoretically, the zones could be placed on some physiographic gradient. However, all zones were rarely or never encountered at one place, since stream action, including water level fluctuation, commonly eliminated one or more zones. These zones were described as the potential of the river floodplain vegetation. Any given species was usually found to occupy an elevational position on one floodplain similar to its position on the floodplain of a different river.

Furthermore, subtle zonation of species density may occur within a single zone of dominance (Lindsay et al., 1961). This is especially true in early stages of vegetation on river bars and islands. It is suggested that such zonation may indicate species tolerances to soil moisture levels. These zones probably vary from year to year as water
levels subside and expose substrates at various times. This may be a function of rain patterns in the watershed.

While, in general, these zonal patterns are thought to represent a vegetational response to a soil moisture gradient and variable lengths of exposure to various positions due to receding water levels, the banks with the longest period of exposure may undergo a greater development, adding an extra zonal pattern (Lindsey et al., 1961). Also, zones 1, 2, 3 and 4 are frequently not encountered because of renewed bank cutting by the current or the lack of sufficient drop in water level for these zones to become established.

Germination and Establishment on Exposed Mud

It has been suggested that community composition on previously flooded substrates is principally determined by the distribution of water borne disseminules on individual sites (Lindsey et al., 1961; McGregor, 1948). However, the role of vegetative propagation and dissemination by other means must also be considered in species establishment (Hall, Penfound and Hess, 1946). In addition to the obvious dispersal action of wind and water, disseminules may be distributed on mudflats by the feet, feathers and excrement of wading birds (Penfound, 1953; Salisbury, 1970).

No one factor or factor complex is universally responsible for germination of all species on exposed mud; however, the various operative factors may be controlled by the water level fluctuation. Buried residual seeds have been shown to play a potential role in the
establishment of plants following exposure of the substrate (Linde, 1969). Germination has been reported from as deep as 30 cm below the surface of exposed muds. Some such seeds may remain viable for decades or longer. Germination characteristics of the seeds of Iowa mudflat species, therefore, warrant some consideration.

Environmental parameters have not been strictly related to weed seed germination requirements, nor are these requirements well documented for mudflat species in Iowa. Species which commonly occur on mud apparently depend upon a high evaporation rate and high light intensities (Salisbury, 1970). It has also been noted that these species exhibit great climatic tolerance while usually appearing markedly sensitive to edaphic conditions. This sensitivity may be manifested directly, in establishment, or indirectly through the influence of soil on the competitive ability of a species (Harper, 1960; Salisbury, 1970).

Several common weed species which may occur on reservoir mudflats have been classified (Martin, 1943) as to time of maximum germination in Iowa as follows:

<table>
<thead>
<tr>
<th>Early spring</th>
<th>Late spring or summer</th>
<th>Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lactuca scariola</td>
<td>Datura stramonium</td>
<td>Capsella bursa-pastoris</td>
</tr>
<tr>
<td>Rumex crispus</td>
<td>Chenopodium album</td>
<td>Lepidium apetalum</td>
</tr>
<tr>
<td>Chenopodium album</td>
<td>Xanthium canadense</td>
<td>Lepidium virginicum</td>
</tr>
<tr>
<td></td>
<td>Hibiscus trionium</td>
<td>Bromus tectorum</td>
</tr>
<tr>
<td></td>
<td>Abutilon theophrasti</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Echinochloa crus-galli</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Setaria viridis</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Amaranthus retroflexus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Digitaria sanguinalis</td>
<td></td>
</tr>
</tbody>
</table>
No particular germination requirements were noted in these tests beyond "suitable moisture and temperature." It was felt, however, that a temperature relationship was inferred, since some species did not germinate at all after the onset of summer temperatures. In a greenhouse experiment, Amaranthus retroflexus and Digitaria sanguinalis germinated best at 100°F (37.7°C) McWilliams, 1965). Another mudflat species, Chenopodium album, germinated best at 55-65°F (12.7-18.3°C). While not conclusive, this is further evidence for a temperature-germination relationship in some species (McWilliams, 1965). The cause of seed dormancy in Polygonum pensylvanicum has been located in the embryo, whereas dormancy in Abutilon theophrasti has been related simply to seed coat impermeability (LaCroix, 1961).

The viability of seeds of Polygonum pensylvanicum and Echinochloa crus-galli have been examined in relation to marsh management (Crail, 1951). Short periods of submergence were found to help break dormancy in these species. Long periods of submergence under natural conditions were found generally to reduce germination. During summer submergence, high water temperatures and low dissolved oxygen conditions were suspected of contributing to decreased viability. In studies of Oklahoma lakes, oxygen was ruled out as a limiting factor in vascular plant establishment (Penfound, 1953). Because published research on Iowa reservoirs is so sparse, no definitive conclusions concerning environmental limitations affecting seed germination on mudflats can be reached.

The seed of woody mudflat species are generally viable for a relatively short period of time (U.S.D.A., 1948). Because of this, woody
seedling establishment on mudflats is probably due largely to the most recent seed crop. Salix interior, Salix amygdaloides, Salix nigra, Populus deltoides and Ulmus americana are reported (U.S.D.A., 1948) to become established at a level corresponding to the water level when the seeds were shed. The following temperature optima and seed dispersal periods are recorded for three of these species:

<table>
<thead>
<tr>
<th>species</th>
<th>night (°F)</th>
<th>day (°F)</th>
<th>seed dispersal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer saccharinum</td>
<td>75 (23.8°C)</td>
<td>85 (29.4°C)</td>
<td>April-mid June</td>
</tr>
<tr>
<td>Salix nigra</td>
<td>70 (21.1°C)</td>
<td>85 (29.4°C)</td>
<td>May-June</td>
</tr>
<tr>
<td>Populus deltoides</td>
<td>68 (20.0°C)</td>
<td>86 (30.0°C)</td>
<td>April-June (ripening)</td>
</tr>
</tbody>
</table>

Other factors may affect woody plant establishment on alluvial substrates. It has been suggested (Thomson, 1947) that high levels of soil carbon dioxide and low oxygen levels may preclude invasion of some alluvial sites by species other than Acer saccharinum, Populus deltoides or Salix spp. Both willow (Salix spp.) and cottonwood (Populus deltoides) are very intolerant of competition. Cottonwood establishment may even be inhibited by a heavy grass sod (Fowells, 1965). While both willow and cottonwood often find ideal conditions for establishment following flood water recession, saturated soil does not promote rapid growth in cottonwood seedlings (Brendemuehl, 1957). This usually results in cottonwood being found at slightly higher elevations than willow. Salix nigra and Salix interior apparently require continuous moisture and usually dominate lower, wetter and less sandy sites than Populus deltoides. Salix interior, however, does not persist, usually dying out before small pulpwood size is reached (Fowells, 1965; Lippert and Jameson, 1964).
Characteristics of Water Level Fluctuation and Species Establishment

Time of drawdown has been shown to be a controlling factor in the establishment of volunteer species on exposed mud. Exposure of mud during May in northern Missouri gave extensive smartweed (*Polygonum* spp.) stands (Crail, 1951). Wild millet (*Echinochloa* sp.) establishment was favored by early June drawdown. In areas exposed in mid and late June, *Cyperus* spp., *Xanthium* spp. and other weeds comprised the bulk of the vegetation (Crail, 1951). A different study in the same part of the state found stands of *Polygonum lapathifolium* to result when drawdown occurred in early June. Summer drawdowns, between July 1 and September 15, produced stands of *Echinochloa crus-galli*, often with *Polygonum pensylvanicum* also being present (Burgess, 1969). These differences may simply reflect the potential variation in vegetation response to drawdown from time to time and place to place.

Although Linde (1969) has concluded that vegetative response to drawdown is dependent upon location and the nature of the residual seeds in the soil, it seems likely that prediction of such response must be based on something more than this. Some species, for instance, appear to require a drawdown for germination to be successful. This has been reported for *Echinochloa crus-galli*, *Polygonum pensylvanicum*, *Polygonum coccineum* and *Ammania coccinea* (Crail, 1951; Hall et al., 1946).

Flood tolerance varies considerably in mudflat vegetation. High water levels for a two week period in the height of the growing season have been used to kill *Ambrosia trifida* and *Xanthium* sp.; however,
Echinochloa sp. is often also killed by such treatment, an undesirable effect in waterfowl and wildlife management areas (Hall et al., 1946). Polygonum coccineum is able to flourish in as much as 10 feet of water, but flowers, fruits and apparently persists when stranded by water recession (Penfound, 1953). Cottonwood, (Populus deltoides), black willow (Salix nigra), sandbar willow (Salix interior), river birch (Betula nigra), American elm (Ulmus americana), red maple (Acer rubrum), alder (Alnus rugosa) and silver maple (Acer saccharinum) are reported as flood tolerant species (McDurmott, 1954). In fact, Alnus rugosa, Populus deltoides and Salix nigra have been shown to exhibit an increased growth rate during short term flooding. In these, as in most woody species, short periods of flooding during the growing season are generally not as lethal as single periods of the same total flooding time (Hall et al., McDurmott, 1954). Susceptibility of trees to flood damage corresponds to the average elevational position of the species above the water level in nature (Lindsey et al., 1961). Observations of permanently flooded woodlands indicate mortality of trees is restricted to levels where water covers the root crown for a period of time. Increment borings show little effect of permanent flooding on growth rates of trees more than two feet above the normal pool level. Although willows are generally believed to be the most flood tolerant trees native to Iowa, cottonwoods have been shown to survive flooding, sometimes for two years and more. Other investigations show considerable variation in the mortality rates of flooded trees (Featherly, 1940; Green, 1947; Kramer, 1951; McDurmott, 1954; Yeager, 1949). While flood tolerant trees are sometimes
grown in reservoir fluctuation zones, these are essentially southern species such as baldcypress, tupelo and red gum (Silker, 1948). The success of these species in Iowa reservoirs is questionable.

**Observed Zonation Patterns**

Zonation patterns in Iowa flood control reservoirs are striking phenomena. These zones appear to approximate contour lines about the flood control pools of the reservoirs. Similar patterns were observed at both Red Rock and Coralville Reservoirs, although the dominant vegetation of individual zones was not necessarily common to both reservoirs. While zonation patterns appeared to be related to elevation or some factor related to elevation, various patterns were observed within the same reservoir system. In general, patterns were found to be most distinct in areas most frequently flooded. This suggests that maturation of vegetation and accompanying autogenic influences make zonal boundaries less clear.

**Red Rock patterns**

Vegetation patterns are not uniform throughout the flood pool. Distinct riparian zonation in the upper reaches of Red Rock Reservoir is largely confined to the original meanders and often flooded areas of the preimpoundment Des Moines River. Most upland trees remaining in the flood control pool after construction were killed by inundation. Agricultural land within the zone of maximum fluctuation is largely reclaimed for cropland between flooding periods. Vegetation near the river channel exhibits a complex pattern, probably representing the repeated
establishment of a relatively simple pattern over time. This pattern, as it was observed in July, 1970, is diagrammatically represented in Fig. 8. Both willow (Salix spp.) and Spanish needle (Bidens spp.) exhibited at least two periods of establishment as evidenced by differential size of plants in the various zones.

Zonation patterns increased in area and strength in areas of the reservoir where flood waters were more active. Observations on zonation were concentrated in these areas of frequent disturbance adjacent to the conservation pool, near and west of, the highway 14 bridge. Apparent mudflat dominance in midsummer is indicated in Fig. 9. Areas immediately above the spring flood level were controlled, in general, by Ambrosia trifida. The mudflats proper were largely covered with Polygonum pensylvanicum seedlings, less than 12 inches in height. Inter-spersed throughout the Polygonum beds, in no discernible pattern, were clumps of Elymus virginiana. Small depressions and swales within this area were heavily colonized in midsummer by seedlings of Abutilon theophrasti.

A variation of mudflat vegetation pattern was found in areas of localized deposition or freezing action, or both. Occasional mounds were encountered, rising as high as two feet above the surrounding mud-flat and extending approximately 20 feet in width. The vegetation of these mounds is unlike that of the surrounding area (Fig. 10). Polygonum lapathifolium and Amaranthus spp. dominate the top of the mound. The side slopes of the mound support a heavy growth of Xanthium. Polygonum pensylvanicum occurs on the toeslope and surrounding mud.
Fig. 8. Zonation pattern near stream channel in the upper reaches of Red Rock, July, 1970
Different sized zones of similar species composition suggest pattern is due to repeated establishment of a few plant groups over time
B. cernua
A. camarscini
C. sp.

S. sp.
P. deltoides
A. sp.
B. cernua

B. sp.
A. sp.
S. sp.

water
Fig. 9. Mudflat dominance in midsummer, 1970, near highway 14 bridge
Apparent relationship of topography and species occurrence is illustrated in simplified diagram. The scale is relative.
Ambrosia trifida

about 1.0 m.

Elymus virginicus
Polygonum pensylvanicum

Abutilon theophrasti
Fig. 10. Species dominance on a mudflat mound
The segregation of dominant species on this typically small mound indicates the influence of relief and drainage on species occurrence.
Polygonum lapathifolium, Amaranthus spp., Xanthium strumarium, Polygonum pensylvanicum
The delayed growing season occurring with late drawdown does not allow for full expression of dominant vegetation until August, or, as in 1972, the vegetation is inundated too often to develop fully before the growing season is over. Apparent species dominance on area I-1 in August, 1971, showed distinctive patterns near each shoreline with the interior of the island being dominated by *Setaria* spp., *Conyza canadensis* and *Polygonum pensylvanicum*. The varying width of the area (Fig. 11) precludes the subjective assignment of precise boundaries to these zones. The tendency for species to segregate within these zones suggests the zones represent a compression of the pattern found along the more gradual slope of area I-2 and discussed elsewhere in this paper. Such segregation was not consistent or complete enough to warrant further breakdown of the observed pattern.

The edge of the mud along the waters of the conservation pool is subject to inundation by a very slight rise in water level. Because of this, the vegetation is kept in a relatively immature state and the zonation is somewhat compressed into narrow bands. Dominance of the ten meters adjacent to the water is diagramed in Fig. 12 as it appeared in June, 1971. *Cyperus strigosus* and *Cyperus dentatus* occurred above the level dominated by *Populus deltoides*. *Salix nigra*, *Salix amygdaloides* and *Salix interior* occurred at a position just below that of the *Populus*. Woody litter on the bare mud was thought to be the result of drifting in on a relatively slight rise in water level after drawdown of spring flood waters. Density of seedling establishment was greatest in a narrow band just above the elevation of the woody litter. This may represent
Fig. 11. Three dimensional drawing of study area I-1
This drawing illustrates the variable shape and relief of mudflat areas. Each of the four transects in this figure varies considerably in length with very small fluctuations in water level.
Fig. 12. Dominance of species on the mud edge, area I-1, June, 1970
Area of greatest seedling establishment occurred just above the drift line.
This area was lower than the well established vegetation zone but high enough
to escape being disturbed by small waves.
Cyperus spp.  
*Populus deltoïdes*  
*Salix* spp.  

zone of greatest seedling establishment  

*Acnida tamariscinus*  
*Rorippa islandica*, unidentifiable grasses, forbs  

litter  

bare mud  

water
the area where seeds were stranded by high water, germination response to a moisture or soil aeration gradient, or a combination of these factors. Seedlings in this zone included Acer saccharinum, Acmida tamariscinus and several unidentified grasses and forbs. The area of bare mud between the stranded woody debris and the water was colonized in July by Bidens spp., Cyperus spp., and Amaranthus spp., seedlings.

A discrete and narrow zone of soft maple (Acer saccharinum) seedlings has been observed along the mud edge at Red Rock. Since the seeds of Acer saccharinum are often water disseminated and the seeds remain viable for only a few days, the soft maple seedlings represent the contour defined by the water level during that brief period. Rarely have soft maples more than one year old been encountered on the Red Rock mudflats.

In the Coralville Reservoir system, a well established zone of Acer saccharinum marks the uppermost extent of the flood control pool. This zone is thought to represent the high water levels of 1960, when the pool level was maintained between 689 and 707 feet above mean sea level for the April 1-August 16 period. Succeeding floods were not sufficient to destroy these plants; however, more recently established soft maple zones at lower levels, were destroyed by flooding.

Apparent dominance along transects I-2.1 and I-2.2 was recorded in mid-August, 1971. The patterns observed in this area are depicted in Fig. 13. Zone 1 occupied the relatively flat shoulder of an old road at the left end of the transect. Amaranthus spp. and Chenopodium album made up the dominant vegetation of this well drained narrow zone.
Ten vegetation zones were recognized in this area based on subjectively determined dominance as follows:

1. *Amaranthus hybridus*, *Chenopodium alba*
2. *Ambrosia trifida* in higher positions within the zone; also *Bidens polylepis* in lower areas
3. *Setaria viridis* dominant with *Bidens* sp. and *Ambrosia trifida* occurring often
4. *Polygonum pensylvanicum* with *Xanthium* sp. and *Conyza canadensis* occurring on higher spots
5. *Setaria viridis* with *Polygonum*, *Conyza* and *Setaria lutescens* as associates
6. *Populus deltoides*
8. *Echinochloa crus-galli*, sometimes mixed with *Salix*, *Bidens*, *Polygonum* or *Populus*
9. *Acnida tamariscinus*, sometimes with *Xanthium* as a codominant
10. *Cyperus* spp.
Zone 2 was dominated by *Ambrosia trifida* on the upper part of the back-slope and *Bidens polylepis* on the lower part of the backslope. Based on dominance, the backslope was considered to be a discrete vegetational zone. *Ambrosia trifida* and *Bidens* spp. were present in varying degrees, all along the slope.

Zone 3 was represented by the toeslope at the edge of the road bank. *Ambrosia trifida* and *Bidens* spp. extended into this area, but *Setaria viridis* was considered the leading dominant. Zone 4 was dominated by *Polygonum pensylvanicum*. Localized areas of slightly higher elevation within the zone supported *Xanthium strumarium* and *Conyza canadensis*. Areas designated as zone 5 were dominated chiefly by *Setaria viridis*. *Polygonum pensylvanicum* and *Conyza canadensis* sometimes became locally dominant, often occurring as clumps. *Bidens frondosa* and *Setaria lutescens* were dominant in depressional areas within this zone. *Populus deltoides* attained dominance in areas noted as zone 6. Zone 7 was comprised of a heavy growth of *Salix* spp. *Salix amygdaloides* was dominant on the upper half of the zone. The lower half, comprised of mixed *Salix* species, supported considerably more biomass than did the upper half of the zone. *Echinochloa crus-galli* was the leading dominant in zone 8. *Salix* species were associated with the dominant species in the upper half of the zone. *Bidens comosa*, *Polygonum pensylvanicum* and *Populus deltoides* occurred in lower part of the zone, sometimes becoming codominant. *Acnida tamariscinus*, while fairly widespread, only became dominant within the narrow area of zone 9. *Xanthium strumarium* was also present in this zone and was a codominant in some localized areas.
Cyperus dentatus and Cyperus strigosus were the dominant species in zone 10. Areas of bare mud occurred near the water's edge.

Coralville patterns

Zonation of vegetation in the flood control pool of Coralville Reservoir, at the University of Iowa's Macbride Field Station, followed a pattern similar to that observed in the Red Rock flood control pool (Fig. 14). Dominant species, however, were different in most cases. The upper limit of the flood control pool was marked by a distinct zone of Acer saccharinum. The upper part of the flood control pool was dominated by Oenothera sp., Verbena hastata and Aster pilosus. Daucus carota and Apocynum sp. were locally dominant in some areas at this elevation. A discrete zone of Populus deltoides was observed just downhill from the Aster zone. In general, the area below this was dominated by Polygonum lapathifolium. Carex spp., Rumex sp., Acnida tamariscinus and Cyperus spp. occurred within the range of elevations occupied by this zone and were occasionally encountered as dominants.

Pattern on road banks

The presence of old road beds on mudflats provides a secondary zonation pattern associated with topographic and substrate change over a very short distance. These old road beds were never found to reflect a simple compression of the zonal pattern found on the mudflats proper. Soil characteristics, including internal and external drainage, fertility levels, bulk density and texture would be expected to vary with the individual road bed.

There is some indication that relative elevation within the flood
Fig. 14. Species dominance based on subjective assessment on the MacBride Field Campus of the University of Iowa at Coralville Reservoir
Acer sp.

Oenothera sp.

Papaver sp.

Aster pilosus

Populus deltoides

Carex sp.

Veronica hastata

Polygonum lapathifolium

Rumex sp.

Achnida sp.

Cyperus spp.

approximately 50 m.

Road

approximately 8 m.
pool may affect the species occurring on the road slopes. Figures 15 and 16 represent dominant vegetation on old road banks within the Red Rock flood pool. While absolute elevations were undetermined, the roadway represented in Fig. 15 was approximately five feet higher than the one represented in Fig. 16. The shoulder of the higher road was dominated by Chenopodium album and Rumex sp. Conyza canadensis was the major species on the backslope. The lower backslope also supported a narrow zone of Populus deltoides. Ambrosia trifida was the dominant species on and immediately adjacent to, the toeslope. With the exception of Populus, the species shown in Fig. 15 are characteristic of the upper parts of the flood control pool where flooding has not occurred for at least two years. This may be a reflection of better drainage on the road banks, allowing species to become dominant in a position lower than that which they usually occupy.

The lower road examined at Red Rock (Fig. 16) supported a greater variety of dominant species than did the higher road. Ambrosia trifida and Bidens spp. dominated the shoulder immediately adjacent to the old pavement. Conyza canadensis and Setaria spp. dominated the upper backslope. A narrow zone of Populus deltoides occurred in a midslope position. Melilotus officinalis was dominant on the lower backslope. The toeslope supported a dense growth of Polygonum pensylvanicum which also dominated the surrounding mudflat.

One roadside examined in the upper reaches of Coralville Reservoir, in Section 25 of Monroe Township, T81N, R8W in Johnson County, showed a similar pattern, although most of the species were different (Fig. 17).
Fig. 15. Species dominance relative to topographic position on an old road bank in the upper part of the flood pool at Red Rock Reservoir
Chenopodium album
Rumex sp.

Coryza canadensis

Populus deltoides

Ambrosia trifida
Fig. 16. Species dominance related to topographic position on an old road bank in the lower part of the flood pool at Red Rock Reservoir.
Road

Ambrosia trifida, Bidens sp.

Coryza canadensis, Setaria spp., an unidentifiable member of the Labiatae

Populus deltoides

Melilotus officinalis

Polygonum pensylvanicum

approximately
Fig. 17. Species dominance related to topographic position on an old road bank in the upper part of Coralville Reservoir
Panicum capillare

Oenothera sp.
Melilotus sp.
Salix eriocephala

Scirpus fluviatilis

Bidens cernua

Achnida sp.  Rorippa islandica
Panicum capillare occupied the upland and shoulder position. Oenothera sp. occurred in a narrow band just below the shoulder position. Melilotus sp. was dominant in the middle of the backslope. Salix eriocephala, the only woody species evident, occurred on the lower backslope. The toeslope was dominated by Scirpus fluviatilis. Below the Scirpus zone, the phenology of species appeared considerably retarded, presumably due to late exposure of sediments. Bidens cernua, occurring as seedlings, was the dominant species on the lower toeslope. Acnida tamariscinus seedlings dominated an area just downhill from the Bidens zone. Rosette seedlings, thought to be Rorippa islandica occupied the lowest, wettest exposed mud in the roadside ditch.

Species Distributions and Pattern Relationships

Plant species and species groups recognized on the Red Rock mudflats in 1971 appear in Appendix F. While some species (e.g. Salix interior) exhibited discrete distribution patterns, other species (e.g. Polygonum pensylvanicum) occurred in most of the plots examined. To relate zonal pattern with distribution of individual species, data were recorded for each species present in each meter segment of transects I-1.1, I-1.3, I-1.4, I-2.1 and I-2.2. These data were subjected to a cluster analysis as previously described. A portion of dendrogram drawn from the analysis of I-1.1 is shown in Fig. 18.

The clustered plots from each transect were separated into groups which seemed to relate to the observed vegetation pattern. These groups are displayed from transects I-1.1, I-1.2, I-1.3, I-1.4, I-2.1 and I-2.2 in Figs. 19, 20, 21, 22, 23 and 24, respectively.
Fig. 18. A part of the dendrograph drawn from the data analysis of transect I-1.1. This dendrograph is the result of clustering the plots of transect I-1.1. Plot numbers are displayed along the side of the figure. The tree-like pattern depicts similarity relationships as computed by this program. Relative similarity is read from the horizontal axis.
Fig. 19. Diagram showing zonation based on cluster analysis results along transect I-I.
Fig. 20. Diagram showing zonation based on cluster analysis results along transect I-1.2
Fig. 21. Diagram showing zonation based on cluster analysis results along transect I-1.3
Fig. 22. Diagram showing zonation based on cluster analysis results along transect 1-1.4
Fig. 23. Diagram showing zonation as determined by cluster analysis along transect I-2.1
ZONE 1
ZONE 2
ZONE 3
ZONE 4
ZONE 5
ZONE 6
ZONE 7
Fig. 24. Diagram showing zonation as determined by cluster analysis along transect I-2.2
The cluster analysis technique was used to separate, or cluster, plots along individual transects into similar groups. The results of such clustering appear as a dendrogram. As such, the entire transect can be thought of as a single group comprised of various levels of subgroups. The level of similarity considered (i.e., the size of subgroup considered meaningful) is arbitrarily chosen. It might be argued that this reduces the objectivity of group definition by this method. On the other hand, the dendrogram does allow the researcher to exercise a preference over a considerable range of otherwise objective classification possibilities.

Because of size limitations of the computer program used, it was not possible to cluster all plots of all transects at the same time. Accordingly, the individual meter square plots of each transect were clustered independently. The accepted level of similarity was comparable, but not precisely the same, for transects within each study area (I-1 and I-2). This inconsistency, in itself, introduces no error into the method, since each data set is of a different size and responds independently to the clustering process. It has been shown (McCammon and Wenninger, 1970) that an increase in the number of samples in a given clustering process tends to reduce the similarity level at which clustering is complete.

As it was used in this study, cluster analysis has one decided disadvantage. While any given cluster is easily defined in terms of the plots which comprise it, no information is available concerning the basis for that grouping. In other words, plots in a transect may be grouped,
but no discrete species list is applicable to that group. The differences responsible for the clustering are not apparent.

Results of clustering of plots along transects I-2.1 and I-2.2 indicate that pattern may partially be attributed to species occurrence. The presence of Populus deltoides and Salix spp., for instance, seems closely associated with zones 7 and 3 of I-2.1 and I-2.2, respectively. Similarly, the shoreline vegetation of both transects was separated from the rest in the cluster analysis. This zone includes species (Cyperus spp., Ammania coccinea, Lindernia dubia) which are restricted to the moist end of the transects. Other clustered zones, notably zones 1 and 2 of both I-2.1 and I-2.2, bear no obvious relationship to observable species distribution. Results of clustering plots of transects in area I-1 were similar. Shoreline species were separated from the rest. Groupings toward the center of the transects did not correspond to observed patterns. Choosing groups from a different level of clustering did not clarify the pattern relationships. This might lead to the assumption that the observed vegetation pattern is due to differences in species dominance, density or even vigor. While such an assumption seems tenable and observations at least do not refute it, any change in the data or difference in the clustering procedure would be expected to give different vegetation groupings. Because of the hierarchical nature of the program used, a very small change might give very different results. One can conclude that some subjectively determined patterns correspond with patterns of species distribution as indicated by this particular analysis. Other subjective patterns show little similarity
to patterns based on distributions, as this analysis computes them.

Inundated and Exposed Soils

Sediments deposited by flood waters appear to contribute to the buildup of reservoir mudflats. Any consideration of these soils should deal with both flooded and exposed characteristics of this substrate. While no literature dealing with this particular system has been found, certain works in limnology, soils and wildlife areas seem partially applicable.

It has long been recognized that the nature of the substratum beneath a body of water has a considerable effect on the vegetation of the system. Some evidence suggests successional patterns on drained impoundments may be controlled by soil type (Moyle and Nielsen, 1953). Certain edaphic parameters have been correlated with the distribution patterns of aquatic plants in English lakes (Misra, 1938). Chemical and biochemical relationships between mud and water in aquatic systems have been investigated by several workers (Cook and Powers, 1958; Irwin and Stevenson, 1951; Mortimer, 1941; Mortimer, 1942).

General trends of floodplain vegetation development may be closely related to the nature of the alluvial substrate and water-level relationship. Having defined the soil-water relationship as the controlling factor in the determination of river floodplain vegetation, Lindsey et al. (1961) attempted to define a gradient in soil texture along two stream courses. Particle size was expected to grade from sand in the upper course to clay in the lower course, reflecting a general decrease in
turbulence; however, this gradient was not well expressed, presumably because of the variability of local conditions under which particles were transported.

Quantitative assessment of the response of vegetation to soil parameters have not been remarkably successful. Elevation, depth of soil development, texture, pH, exchangeable calcium, potassium and magnesium explained less than 14 percent of the variation attributed to successional stages on a drained lake bed in Tennessee (DeSelm and Shanks, 1967). In a more aquatic situation on the Back Bay National Wildlife Refuge, no significant correlation was found between pH, organic matter content, available phosphorus or available potash in the substratum and the amount of plant growth (Chamberlain, 1948).

The distribution of some floodplain species may relate to soil texture. *Acer negundo* has been found in sandy river floodplain soils near the water (Lindsey et al., 1961). This soil texture would simulate the well drained soils which Lindsey associated with the occurrence of the species. On a drained lake bed in Tennessee, *Salix* thickets occurred at 11 of 12 points where the soil clay ranged from 14-25 percent and moisture was available (DeSelm and Shanks, 1957). A less obvious effect of substrate on plant distributions occurs as a reservoir muds dry and crack. This cracking disturbs small rooted plants and sometimes provides a favorable microclimate for liverworts (Lindsey et al., 1961).

Wetland soils are greatly affected by fluctuation of water level. If that fluctuation exposes the soil, as is the case in flood control reservoir mudflats, increased aeration changes the chemical, physical
and biotic aspects of the substrate. The literature relating to these effects has recently reviewed by Phillips (1970). A reduction in the exchange capacity along with the formation of acidic humic colloids may often accompany aeration and drying of waterlogged soils (Pearsall, 1950). These microbiologically inert iron-humus complexes may have long term implications for the productivity of reservoir mudflats.

Periodic "drawing down" of impoundments is often done to increase primary productivity, particularly in managing for waterfowl (Weller and Spatcher, 1965). An increase in primary productivity brought about by drawdown and reflooding is generally thought to be a result of the release of organic material to aerobic decomposition (Hartman, 1949; Harris and Marshall, 1963; Kadlec, 1962; Sanderson and Bellrose, 1969). While reflooding of aerated wetland soils is known to produce increases in organic matter, pH, available calcium, magnesium, manganese, potassium, iron and aluminum, this may be an ephemeral condition. Furthermore, frequent drawdowns may actually flush away nutrients and ultimately decrease productivity in those total lake systems which depend upon leaching of nutrients into the system to support production (Cook and Powers, 1958; Harris and Marshall, 1963).

Soil Characteristics

Deposition of silt on reservoir mudflats may vary from place to place, but observations at Red Rock indicate yearly increments of 10 cm and more to be possible. Several inches of silt have been deposited at various times on the abandoned segment of highway 14 within the flood
pool; the root crown position of second year *Populus* seedlings indicates localized deposition in excess of 15 cm to be common on the mudflats. This material may be dropped by the slow moving waters of the flooded river as they enter the reservoir or reflect localized erosion and deposition on the same or adjacent areas of mudflat. Because of this depositional and erosional aspect, soil analysis associated with this study may reflect the nature of these sediments more closely than the characteristics of the previously described soils of the area. Results of these analyses are presented in Appendix G.

Soil textures were largely in the silty clay loam range in areas I-1 and I-2. Greatest fluctuations were observed in the sand and clay fractions of the particle size analysis. These changes appear to be generally, if not consistently, associated with slope characteristics along the gentle relief of the mudflat. The relative amount of clay in the top 5 cm appears to be generally less in areas of steeper slope, except at the edge of standing water. The sand and silt fractions are less obviously related to topography. Particle size distribution on steep slopes, especially constructed slopes, may vary greatly compared with reservoir deposits which reflect sediment load, duration of flooding, local runoff and erosion since the last deposition. The areas of most extreme particle size variation also seem to be the areas where the most distinctive zonation patterns occur.

Other soil parameters were even less useful than texture in explaining pattern of the vegetation. Percent soil moisture and conductivity were generally inversely related to topographic position; maxima
occurred near the water's edge. Soil organic matter content (expressed as percent loss on ignition) fluctuated, not with elevation, but with steepness of slope and percent clay. Soil pH values were all slightly acid ranging between 5.1 and 6.8. The ends of all three transects were slightly more alkaline than the centers in spite of the fact that the upper end of I-2.1 was the highest topographic point examined.

Determination of soil nutrients in the upper 5 cm of substrate shows that sediments added to mudflats are very low in nitrogen and potassium. The soil solution near the water's edge is continuous with the water of the lake more frequently than is the soil solution of the rest of the mudflat surface, due to slight fluctuations in the lake level and the action of wind and waves. The nutrient values for those samples taken near the water's edge are undoubtedly affected not only by the nutrient content of the water, but also by the materials stranded on the mud. It would seem that this effect might be brought about directly (e.g., by the breakdown of the stranded remains of an algal bloom) or indirectly (e.g., by the improvement of habitat for soil microorganisms under drifts of woody debris). Such aspects of nutrient cycling, however, are mainly conjecture and have not been measured in this study.

Variation in nutrient values along established transects were inconclusive. Nitrate nitrogen values ranged between 0.5 and 8.5 ppm. The higher values (above 2.0 ppm) always occurred at or near the waterline. Nitrates seemed to accumulate within depressional areas along the transects examined. This may simply represent the effects of litter accumulation and greater moisture in these lower areas.
Phosphorus was available in relatively large quantities in the surface substrates of the mudflat. Available phosphorus values ranged from 5.0 to 60.0 ppm with lower values being associated with wetter sites.

Available potassium was less variable, ranging from 103 to 233 ppm in mudflat soils. No obvious topographic relationship was observed.

While variation in some soil parameters, as measured in this study, correspond roughly to changes in topographic relief, these variations are of little help in explaining the observed zonation patterns. Although it is tempting to conclude that variation in these parameters is inconsequential across mudflats, it must be remembered that the data reported here represent an instantaneous measurement in the uppermost layers of soil. More extensive investigations are needed to characterize various depths of the soil profiles of these areas. Also, information on the depth of the root zone, soil effects on plant-water relationships and the nature of soil development with time might be useful in an explanation of mudflat vegetation pattern. However, the strong vegetation pattern of the study areas is reflected only very weakly in the soil parameters as measured in this study.

Succession on Exposed Substrates

The occurrence of predictable sequences of species replacement in areas with fluctuating water levels is not recognized by all who have worked with this system. Relatively little information is available on
changes in species dominance of mudflat vegetation in lakes with extreme water level fluctuations (Tiemeier, 1951). In fact, Penfound (1953) has ruled out the possibility of succession in such zones because of the reoccurring disturbance of inundation and drying.

On the other hand, Meeks (1969) reported that aquatic and semi-aquatic plants were replaced by annual weeds in certain managed wetlands. This replacement progressed faster when drawdown occurred every year. Stands of Polygonum have been reported elsewhere (Linde, 1969) to give way to Bidens and Typha in some shallow aquatic systems with fluctuating water levels. Typha was found to invade deeper water with successive drawdowns. Repeated exposure of substrates in other areas has allowed sedges to invade mudflats and compete with established stands of smartweed (Polygonum) and millet (Echinochloa) (Linde, 1969).

It has been suggested (Lindsey et al., 1961) that transfer of dominance in riparian succession is generally related to the rise in level of the substrate which results in more regular drainage and soil aeration. This implies that allogenic factors (e.g., sedimentation rates) are probably most important in early stages of riparian community development, with autogenic factors becoming more important as development progresses.

Backwater pocket succession patterns are reported for river systems (Lindsey et al., 1961). This sequential development typically begins with a Sagittaria bordered invagination of the shoreline. Acer saccharinum and various Salix species are typical early invaders. If the backwater area is extensive and sedimentation is great, a
grass-sedge and perennial forb zone may persist for a time until the flood plain forest encroaches.

Pioneer plant communities along floodplains may vary considerably (Lindsey et al., 1961). Annual grass-Polygonum-Acnida communities were reported as pioneer vegetation on river mud banks. An Acer-Salix-Populus associations was reported on a higher bar position. Temporarily flooded old fields have been found to support Xanthium strumarium, Polygonum pensylvanicum and Setaria viridis as dominant species. Further succession on such areas results in a dense community of tall flowering perennial forbs and invading tree seedlings. Once this stage is reached, severe flooding is required to induce regression (Lindsey et al., 1961).

In examining similar successional patterns on drained impoundments, Robinton and Burk (1972) found some species of seral communities to be common to both secondary terrestrial and primary hydrarch succession. It was suggested that this overlap may constitute a stabilizing force which would assure rapid vegetative cover of the substrate when the environment is disrupted. Furthermore, it was suggested that this force may be at work in marsh and river floodplain seral stages.

Although frequent flooding seems to promote annual communities, observations indicate that numerous perennial species invade and persist on flood control reservoir mudflats. Establishment of Sagittaria latifolia was observed at several locations within the zone of frequent inundation at Red Rock. In each case, establishment appeared to be related to propagule availability. Sites of colonization occurred in backwater areas of probable deposition, at the junction of small drainage
systems and the reservoir or on the inside curves of the river channel. This was thought to be a function of reduced bank erosion; the position of the new colony representing an area where water borne propagules could develop a supporting root system. Such colonization bears a striking similarity to initial stages of backwater pocket succession as described by Lindsey et al. (1961).

It has been suggested (Van Dyke, 1972) that marsh species (e.g., *Sagittaria* spp.) cannot persist in areas of extreme water level fluctuation. Observations at Red Rock raise serious questions as to the predictability of the success of wetland species in such an area. On June 14, 1971, two small clumps of *Sagittaria latifolia* were observed on a newly exposed mudflat just downstream of the highway 14 bridge on the north side of the river channel. By midsummer, 1972, this mudflat was well colonized by *Sagittaria*. Following an August inundation of two weeks duration, these plants were observed to survive and produce new vegetative growth. It is possible that such a stress, occurring near the end of the growing season, will not leave sufficient energy in the storage organs of the plant to insure survival until the 1973 growing season. Until further observations are possible, statements on long term success of this species are speculative.

Low areas within the floodplain expanse, representing river meanders and oxbow lakes of a previous time, support a vegetation which typically includes several wetland species. Zonation of perennials in such areas does not closely follow the contours of the conservation pool. Local topography tends to control the occurrence of zones. *Eleocharis* sp.,
Juncus sp., Sium suave, Scirpus spp., Verbena hastata and Spartina pectinata were observed where a system of old river meanders occurs within the Red Rock flood pool in Section 3 of Union Township, T76N, R20W, in Marion County. The extent of development of this vegetation indicated that the establishment of these species probably predated the filling of the reservoir. The presence of these species within the flood pool during the summer of 1971 suggests that a potential for perennial semiaquatic vegetation does exist within the zone of water level fluctuation.

The prediction of successional trends in mudflat vegetation is a hazardous endeavor. Willow thickets (Salix spp.) established on the mudflats near and west of the highway 14 bridge at Red Rock in 1969 have increased in area with each successive growing season (Fig. 25). Associated with these thickets, in a slightly higher topographic position, stands of cottonwood (Populus deltoides) persist. Because season, depth and duration of flooding on reservoir mudflats are not highly predictable, it is not possible to determine how many years these species are likely to survive.

Species replacement appears to occur in some situations but the governing conditions for such replacement are not precisely known. The depth and duration of a given flood will, at least in part, be reflected in the severity of vegetation disturbance. When flooding is severe enough to completely destroy existing vegetation, species replacement seems likely to occur. The season of flooding also appears to have considerable effect on species change. Mollugo verticillata, for example,
Fig. 25. Photograph of extensive *Salix* stand on Red Rock mudflats, looking southeast from the north portion of highway 14 bridge in midsummer.
was a common colonizer of bare mud at Red Rock in 1970, but was encountered only rarely in 1971, in spite of an abundance of similar habitat. The major flood period of 1970 occurred in May at Red Rock (Fig. 26). In 1971, the reservoir flood waters were released by mid-April. This difference in time of exposure, and concomitant differences in photoperiod and temperature, would result in different conditions for germination of mudflat species. Unfortunately, critical information on germination requirements for most of these species is not available. Critical qualitative observations on Iowa mudflats are needed to document species germination over a range of flooding situations.

The availability of propagules of a species immediately following flood water recession probably has a significant effect on mudflat vegetation. Since regrowth of existing vegetation and establishment of new species occurs rapidly on newly exposed mudflats, the success of a species whose propagules reach the mudflat late in the growing season may be limited by the competition of established species. This effect of competition on establishment is well documented with respect to cottonwood establishment (Fowells, 1965), but similar information is unavailable for most mudflat species.

Experimental Planting

Experimental plantings in two areas, P-1 and P-2 (Fig. 7), at Red Rock were not generally successful. *Andropogon gerardi*, *Cyperus esculentus*, *Echinochloa crus-galli* var. *frumentacea*, *Panicum virgatum*. 
Fig. 26. Water level fluctuations for Red Rock Reservoir during 1969, 1970 and 1971

Gage readings at Red Rock dam for the first, tenth and twentieth day of each month furnished by, and used with the permission of, the Rock Island District, U.S. Army Corps of Engineers, Rock Island, Illinois
Elevation (MSL)

Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec

1969
Fig. 26 (Continued)
Fig. 26 (Continued)
Phalaris arundinacea, Polygonum pensylvanicum and Zizania aquatica were sown in duplicate, 11 x 66 foot plots with the main axis perpendicular to the water's edge. Planting was done June 1 and 22, 1971 at P-1 and June 4 and 28, 1971 at P-2. These areas were examined for species establishment and survival during and near the end of the 1971 growing season.

Several factors frustrated species establishment and later attempts at assessment of planting success. During and immediately following the planting procedure, numerous unidentified shore birds were observed feeding on the seed. Because the size of the plots was small (11 x 66 feet) and it was not practical to cover the seeds, the extent of predation on the seeds may have been substantial.

Another problem encountered dealt with the fluctuation of the water table in the upper part of the reservoir. Plantings on the margin of a pool were often many yards from open water a few weeks after planting. This inconstant water level made it impossible to recognize any response to a moisture gradient within a plot.

Assessment of planting success was further complicated by the natural occurrence of several of the planted species on the area. While dominance of these species did not exhibit a marked increase in the planted plots as compared with the unplanted areas, the percentage of seed failing to germinate is not known.

The only case of unqualified planting success occurred with Japanese millet (Echinochloa crus-galli var. frumentacea). Establishment and seed production were observed in pure to nearly pure stands in both
planting areas P-1 and P-2. In a preliminary examination, six subjectively randomized 20 x 50 cm quadrats were clipped at ground level, oven dried and weighed. Three such plots of the planted millet averaged 1598 grams/m². Three similar plots of naturally occurring *Echinochloa crus-galli* averaged 2229 grams/m². The plots of naturally occurring millet also contained *Polygonum pensylvanicum*, *Cyperus strigosus*, *Setaria viridis* and *Leersia oryzoides* as subdominants. Clipping was done on September 9, 1971, after some seed shatter had occurred.

Attempts at comparing seed production were abandoned because of excessive seed shatter and bird predation on the seeds. The extent to which these factors affect the above estimates of standing crop is not known, but is thought to be relatively small when compared to total standing crop estimates. The planted variety of *Echinochloa* (Japanese millet) produces a distinctive seed head which is much denser and more compact than that of the local *Echinochloa crus-galli*. Japanese millet is recognized as a highly desirable species on waterfowl areas; natural reseeding from a planted population, however, occurs at a very low rate (Crail, 1951; Burgess, 1969).

While observations on Japanese millet are not conclusive, they indicate that stands of planted *Echinochloa* may be able to produce heavy waterfowl food crops and control the growth of noxious weeds by competition. Because less organic matter is involved than is the case in naturally occurring plant communities, Japanese millet seems worthy of consideration in any mudflat management scheme where annual planting is involved. The relatively low biomass production of the species is not
an unattractive attribute of the species. The encouragement of a species with relatively low productivity on mudflats would be expected to result in a reduction of total organic matter added to the reservoir with each flood period. The implications of such a reduction are not clear; the net effect would seem to have some potential for restricting the influx of organic nutrients into the permanent pool of the reservoir and thereby increasing water quality.

On the other hand, the high flushing rate of the reservoir compared to the relatively slow breakdown rate of plant material may make the fertilizing effect nonexistent. Alternately, extensive nutrient reserves in sediments (Odum, 1971) are said to be important stabilizing factors in ecosystem dynamics. Recently, estuarine systems, where daily water level fluctuations occur, have been shown to possess nutrient reserves far in excess of that required for stability (Pomeroy, Shenton, Jones and Reinhold, 1972). Such nutrient reserves theoretically enable an ecosystem to withstand periods of adverse conditions (e.g., flooding) with less perturbation than a similar system which lacked such nutrient reserves. In the long run, then, perhaps management techniques should not attempt to minimize organic production. Perhaps management should add nutrients from outside sources, encourage productivity and attempt to incorporate these nutrients into the substrate between flood periods. Would such management encourage perennial wetland species and thus speed succession? Would this provide, in turn, a sediment trap which might prolong the life of the reservoir? How would long and short term water quality be affected? Such questions point out the limitations of present knowledge in this area.
SUMMARY AND CONCLUSIONS

Extensive areas within the flood pools of Iowa flood control reservoirs are subject to periodic inundation by flood waters. Mudflats, occurring where gently sloping land areas are frequently inundated, typically support weedy vegetation which occurs in distinctive zonation patterns. This study combined general observations with transect studies, at Red Rock Reservoir in central Iowa, to document vegetation patterns and relate those patterns to measureable ecotope variation, with the following results:

1) Zonation patterns appeared to be similar in Red Rock and Coralville Reservoir flood pools during 1970 and 1971, although the species involved were not necessarily the same.

2) Zonation patterns, based on subjectively determined species dominance, were documented. These patterns were related to patterns along precisely defined transects determined by a cluster analysis technique using similarity of species composition. Some, but not all, of the subjective pattern was explained by this analysis of species distribution. Differences in density, phenology and vigor were not quantified, but appeared to influence the definition of subjective pattern.

3) The upper layer of mudflat substrate at Red Rock was typically silty clay loam, having low levels of available potassium and nitrate nitrogen. Variations in soil parameters, including texture, nitrate nitrogen, available phosphorus and potassium,
pH, conductivity, soil moisture and organic matter content, did not closely correspond to pattern in the vegetation.

4) Species replacement in mudflat vegetation is not well documented. Observations indicate that the time of mudflat exposure may determine the potential vegetation of an area through environmental effects on seed germination. The presence of perennial wetland species within the fluctuation zone indicates the possibility of hydrarch succession on reservoir mudflats.

5) Limited experimental plantings on reservoir mudflats indicate the potential of *Echinochloa crus-galli* var. *frumentacea* in a management scheme involving annual planting; no recommendation is made concerning such management.

6) Management of flood control reservoirs demands critical quantitative information regarding dynamics of the mudflat ecosystem. Information from this study may provide a basis for further much needed research in this poorly understood area.


Martin, J. N. 1943. Germination studies of the seeds of some common weeds. Iowa Academy of Science Proceedings 50:221-228.


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APPENDIX A: AUTHORITY$^2$ AND PHYSICAL DATA PERTINENT TO RED ROCK AND CORALVILLE RESERVOIR PROJECTS

$^2$Appendix A is based on information furnished by and used with the permission of the U.S. Army Corps of Engineers, Rock Island District, Rock Island, Illinois.
AUTHORITY FOR THE RED ROCK PROJECT

Public Law 761, 75th Congress, 3rd Session, approved the general comprehensive plan for flood control and other purposes in the Upper Mississippi River Basin, described in House Flood Control Committee Document No. 1, 75th Congress, 1st Session. General Design Memorandum No. 4, dated 10 January 1958, contains additional information relative

AUTHORITY FOR THE CORALVILLE PROJECT

The Coralville Reservoir project was selected by the Secretary of the Army and the Chief of Engineers under authority granted in Section 4 of the Flood Control Act of 28 June 1938 (Flood Control Committee Document No. 1, Seventy-fifth Congress, 1st session).
ENGINEERING DATA
CORALVILLE RESERVOIR AND DAM

Purpose of Project
Flood Control, Low Flow Augmentation, and Incidental Benefits to Recreation and Fish and Wildlife

Location of dam
Stream Iowa River, Iowa
River mile above mouth 93.3
County Johnson
Nearest town Iowa City, Iowa

Location of reservoir
River mile above mouth 93.3 - 128.3
Counties Johnson, Linn and Iowa

Drainage area
Upstream from damsite 3,115 square miles
Upstream from mouth 12,637 square miles

Reservoir
Elevation of top of flood control pool (spillway crest) 712.0 m.s.l.
Elevation of top of conservation pool
15 February - 15 June 670.0 m.s.l.
Elevation of top of conservation pool
15 June - 15 February 680.0 m.s.l.
(For wildlife purposes  
25 Sept. - 15 Dec.)  

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**PROJECT FACTS**

**RED ROCK DAM AND LAKE RED ROCK**

**Purpose**

Flood Control, Low Flow Augmentation, and Incidental Benefits to Recreation and Fish and Wildlife.

**Location**

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**Dam**

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**Reservoir**

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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Flood control pool</td>
<td>33.5</td>
</tr>
<tr>
<td>Lake Red Rock</td>
<td>11.3</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Water surface elevation (feet above sea level):</th>
<th></th>
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</thead>
<tbody>
<tr>
<td>Flood control pool</td>
<td>780</td>
</tr>
<tr>
<td>Lake Red Rock</td>
<td>725</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Area in acres:</th>
<th></th>
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</thead>
<tbody>
<tr>
<td>Flood control pool</td>
<td>65,500</td>
</tr>
<tr>
<td>Lake Red Rock</td>
<td>8,950</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Storage volume, acre-feet</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Flood control pool</td>
<td>1,740,000</td>
</tr>
<tr>
<td>Lake Red Rock</td>
<td>90,000</td>
</tr>
</tbody>
</table>
APPENDIX B: OPERATIONAL PLANS\textsuperscript{3} FOR RED ROCK AND CORALVILLE RESERVOIRS

\textsuperscript{3}Appendix B is based on information furnished by and used with the permission of the U.S. Army Corps of Engineers, Rock Island District, Rock Island, Illinois.
PLAN OF OPERATION - Red Rock Reservoir

The plan of operation will consist of storing excess flows of the Des Moines and Raccoon Rivers. The reservoir will be operated essentially in tandem with the Saylorville Reservoir, presently under construction 70.8 miles upstream, also on the Des Moines River.
PLAN OF OPERATION - Coralville Reservoir

The primary purpose for which the project was authorized is flood control. The plan of operation is designed to effect reductions of flood crests on the lower Iowa River and on the Mississippi River below the confluence of the two streams without the use of surcharge storage. The reservoir regulation plan which has been selected is designed to provide the greatest overall downstream flood control benefits and at the same time give maximum consideration possible to recreational interests and water quality control below the dam. Insofar as practicable, discharge rates will be adjusted to assure that the water level in the reservoir does not exceed elevation 712.0. A conservation pool will be maintained at a minimum elevation of 670.0. When natural flow in the Iowa River below the dam is less than 150 cfs, storage in the conservation pool will be released to maintain a minimum flow of 150 cfs. The conservation storage pool will be maintained at elevation 670.0, or as near that elevation as practicable, during the period between 15 February and 15 June when maximum storage for flood control is needed. From 15 June to 25 September, the possibility of floods is more remote and the conservation pool will be held to elevation 680.0. The primary purpose for this additional storage is to provide for the minimum release of 150 cfs during prolonged periods of natural low flow. From 15 September to 15 December the conservation pool will be raised to elevation 683.0 if inflow conditions permit. This phase of regulation is in compliance with requests of the Iowa Conservation Commission and is designed to facilitate waterfowl management on the reservoir. The maintenance of the pool at elevation 683 is accomplished during a period of the year when low inflow is normally expected. From 15 December to 15 February the conservation pool will be maintained at elevation 680.0.
APPENDIX C: WATER QUALITY DATA FROM THREE POINTS NEAR THE RED ROCK CONSERVATION POOL LEVEL, AUGUST 19 AND 20, 1971
Fig. C-1. Diurnal curve of water temperature variation at three points near the Red Rock conservation pool, August 19-20, 1971
Fig. C-2. Diurnal curve showing pH variation of water samples from three points near the Red Rock conservation pool level, August 19-20, 1971
Fig. C-3. Diurnal curve showing variation in dissolved oxygen of water samples from three points near the Red Rock conservation pool, August 19-20, 1971
DISSOLVED OXYGEN (ppm)
Fig. C-4. Diurnal curve showing variation in phenolphthalein alkalinity of water samples from three points near the Red Rock conservation pool, August 19-20, 1971
PHENOLPHTHALEIN ALKALINITY
as ppm CaCO₃

TIME in hours
Fig. C-5. Diurnal curve showing variation in total alkalinity of water samples from three points near the Red Rock conservation pool, August 19-20, 1971
TOTAL ALKALINITY

as ppm CaCO₃

TIME in hours

1200 1400 1600 1800 2000 2200 2400 2600 2800 3000 3200
APPENDIX D:  DESCRIPTIONS OF SOIL TYPES OF THE RED ROCK RESERVOIR FLOOD POOL
Soil type number 354 Marsh

**Soil Description:**

Marsh is depressions or flats intermingled with ponds where the water table is at or near the surface the year around. The natural vegetation consists of cat-tails, rushes, sedges, and other water-tolerant grasses.

Marsh has no distinct soil layers. When the water recedes, a layer of old plant residues can be seen at the surface. The surface layer is 8-14 inches of very dark gray mucky silt loam. The sub-stratum is light gray medium silty clay loam to light silty clay with olive mottles.

Soil type number 315 Alluvial land

**Soil Description:**

This soil is on bottomland floodplains adjacent to stream channels. Individual areas are long and narrow in shape and 10-60 acres in size.

Alluvial land consists of recently deposited, highly stratified sediments that have not been in place long enough for soil to develop. The sediments vary in texture but are mainly loam, sandy loam and silt loam, and are typically dark grayish brown and brown in color.

Included in mapping are areas of dark grayish brown and grayish brown silt loam with no sandy loam or loamy sand at less than 40 inches, a few areas of very dark grayish brown silt loam over sand at less than 40 inches, and a few small areas of nearly pure gravel.

Soil type number 220 Nodaway silt loam

**Soil Description:**

The Nodaway series consist of moderately well drained, silty, bottomland soils. They have formed in recently deposited, stratified, silty alluvium on first bottom lands. These soils are young enough that vegetation has not influenced soil formation. They are frequently flooded and receive new deposits of silt with each flood. Nodaway soils are nearly level, but some areas may be slightly undulating due to remanents of the old meandering stream channel.

Nodaway soils typically have a dark grayish brown silt loam surface layer about 7 inches thick. Beneath this is a stratified, grayish brown and dark grayish brown silt loam with a very few thin strata of silty clay loam that extend to a depth greater than 60 inches.
Soil type number 220  Nodaway silt loam (Continued)

Nodaway soils are suited to intensive row cropping when adequately protected from flooding. Most flooding occurs before row crops are planted. Some areas are dissected by channels or intermittent streams extending from the uplands.

Soil type number 467  Radford silt loam

Soil Description:

The Radford series consists of dark colored, somewhat poorly drained, silty soils. They formed in recently deposited, stratified alluvium. They are of such recent age that vegetation has had little effect on soil morphology. They occur in the narrower flood plains, waterways, and less commonly in the broad river bottoms. Radford soils have a very dark grayish brown silt loam surface layer and a stratified, very dark brown silt loam substratum. At depths of 2 or 3 feet the stratified layer is underlain by a black or very dark gray, silty clay loam buried soil. These soils are productive but generally require artificial drainage for optimum crop growth. They are subject to seasonal flooding. Radford soils are well suited to corn, soybeans, and meadow. Some are used for pasture.

Soil type number 88  Nevin silty clay loam

Soil Description:

The Nevin series consists of dark colored, somewhat poorly drained silty soils. They formed in silty alluvium under a native vegetation of prairie grasses. They are on nearly level to gently sloping low stream benches or second bottoms. Nevin soils often occupy broad areas that slope gradually toward alluvial flood plains. Nevin soils typically have a black, silty clay loam surface layer about 24 inches thick. The subsoil to a depth of about 52 inches is mainly a dark grayish brown, silty clay loam that has mottles in the lower part. The substratum below a depth of 52 inches is mottled brown silty clay loam. Nevin soils are well suited to corn, soybeans, small grains, and hay. Most areas are cultivated. The Nevin soils are slightly higher in elevation than the adjacent first bottoms and generally do not flood. Areas adjacent to flood slopes may receive runoff.

Soil type number 133  Colo silty clay loam

Soil Description:

The Colo series consists of dark colored, poorly drained, bottomland
Soil type number 133 Colosilty clay loam (Continued)

soils which have developed in moderately fine textured alluvium. They occupy stream bottoms throughout Iowa and are subject to flooding. Some Colo soils occur on gentle slopes at the base of upland slopes. The Colo soils have thick, black, silty clay loam surface layers and moderately slowly permeable, very dark gray, silty clay loam subsoils. They are typically neutral in reaction and are underlain with coarser textured sediment at a depth of 4 feet or more in some places. The Colo soils are well suited to intensive row cropping and are very productive, although artificial drainage and flood protection may be needed in some areas.

Soil type number 485 Spillville loam

Soil Description:

Spillville series consists of dark colored moderately well to somewhat poorly drained loamy soils. They have developed in loamy alluvium under the influence of grass vegetation. They occur on nearly level drainageways and bottomlands.

The surface layer is a black to very dark brown loam which extends to a depth of more than 36 inches. These soils are moderately permeable. They are generally slightly acid to neutral in reaction.

If these soils are protected from runoff and flooding they are highly productive and well suited to row crops. These soils are subject to flooding. However, stream channels deepening and straightening, road ditches and road construction have modified the flooding pattern hazard of many streams. Each area will vary in its needs for flood protection.
APPENDIX E: U.S. GEOLOGICAL SURVEY AIR TEMPERATURE DATA FROM KNOXVILLE, IOWA, ABOUT FIVE MILES SOUTH OF THE RED ROCK FLOOD POOL, AND SOIL TEMPERATURE DATA FROM AMES, IOWA
Fig. E-1. Graph showing U.S. Geological Survey air temperature data from Knoxville, Iowa, and soil temperature data from 4 inches below the surface at Ames, Iowa, during 1969, 1970 and 1971.
Fig. E-1 (Continued)
Fig. E-1 (Continued)
APPENDIX F: A LIST OF PLANT SPECIES ENCOUNTERED IN MUDDFLAT TRANSECT STUDIES AT RED ROCK RESERVOIR, 1971
Abutilon Theophrasti Medic.
Acer saccharinum L.
Acnida tamariscinus (Nutt.) Wood
Amaranthus hybridus L.
Amaranthus retroflexus L.
Ambrosia artemisiifolia L.
Ambrosia trifida L.
Ammannia coccinea Rottb.
Apocynum androsaemifolium L.
Asclepias sp. L.
Aster Pilosus Willd.
Aster simplex Willd.

Bidens cernua L.
Bidens comosa (Gray) Wiegand
Bidens frondosa L.
Bidens polylepis Blake
Boltonia latisquama Gray

Carex suberecta (Olney) Britton
Carex sp. L.
Chenopodium album L.
Convolvulus sp. L.
Conyza canadensis (L.) Cronq.
Cyperus dentatus Torr.
Cyperus strigosus L.

Echinochloa crus-galli (L.) Beauv.
Eleocharis sp. R. Br.
Elymus virginicus L.
Eragrostis cilianensis (All.) Lutati

Hibiscus Trionium L.
Hordeum jubatum L.

Impatien pallida Nutt.
Ipomoea hederacea (L.) Jacq.

Lactuca sp. L.
Leersia oryzoides (L.) Swartz
Lepidium sp. L.
Lindernia dubia (L.) Pennell
Lippia lanceolata Michx.
Lycopus americanus Muhl.

Melilotus alba Desr.
Melilotus officinalis (L.) Desr.
Mimulus ringens L.
Oenothera biennis L.

Panicum capillare L.
Panicum dichotomiflorum Michx.
Penthorum sedoides L.
Phalaris arundinacea L.
Physalis virginiana Mill.
Physostegia virginiana (L.) Benth.
Polygonum lapathifolium L.
Polygonum pensylvanicum L.
Populus deltoides Marsh.

Rorippa islandica (Oerder) Borbas
Rumex sp. L.

Salix amygdaloides Anderss.
Salix eriocephala Michx.
Salix interior Rowlee
Salix nigra L.
Scutellaria lateriflora L.
Setaria lutescens (Weigel) Hubb.
Setaria viridis (L.) Beauv.
Solanum carolinense L.

Trifolium pratense L.
Typha angustifolia L.
Typha latifolia L.

Xanthium strumarium L.
APPENDIX G: DATA ON MUDFLAT SUBSTRATE CHARACTERISTICS, RED ROCK RESERVOIR, IOWA
Fig. G-1. Nitrate nitrogen values for the top 5 cm of soil along transects I-1.1, I-1.3 and I-2.1
Fig. G-1 (Continued)
Fig. G-1 (Continued)
Fig. G-2. Available phosphorus in the top 5 cm of soil along transects I-1.1, I-1.3 and I-2.1
Fig. G-2 (Continued)
AVAILABLE PHOSPHORUS (ppm)

Fig. G-2 (Continued)
Fig. G-3. Available potassium in the top 5 cm of soil along transects I-1.1, I-1.3 and I-2.1
Fig. G-3 (Continued)
Fig. G-3 (Continued)
Fig. G-4. Particle size of the upper 5 cm of soil along transect I-1.1

PERCENT SAND
particle size .05−2.0 mm.

PERCENT COARSE SILT
particle size .02−.05 mm.

PERCENT FINE SILT
particle size .002−.02 mm.

PERCENT CLAY
particle size less than .002 mm.
Fig. G-5. Particle size of the upper 5 cm of soil along transect I-1.3

PERCENT SAND
  particle size .05–2.0 mm.

PERCENT COARSE SILT
  particle size .02–.05 mm.

PERCENT FINE SILT
  particle size .002–.02 mm.

PERCENT CLAY
  particle size less than .002 mm.
Fig. G-6. Particle size analysis of the upper 5 cm of soil along transect I-2.1
PERCENT SAND
particle size 0.5-2.0 mm

PERCENT COARSE SILT
particle size 0.02-0.05 mm

PERCENT FINE SILT
particle size 0.002-0.02 mm

PERCENT CLAY
particle size less than 0.002 mm
Fig. G-7. Percent moisture in the top 5 cm of soil along transects I-1.1, I-1.3 and I-2.1
Fig. G-7 (Continued)
Fig. G-7 (Continued)
Fig. G-8. Conductivity of the top 5 cm of soil along transects I-1.1, I-1.3 and I-2.1
ELEVATION in FEET

DISTANCE in METERS

CONDUCTIVITY (mhos x 10^{-5} / cm.)
Fig. G-8 (Continued)
Fig. G-8 (Continued)

CONDUCTIVITY (mhos x 10^{-5}/cm.)
Fig. G-9. Results of pH determination of the top 5 cm of soil along transects I-1.1, I-1.3 and I-2.1
Fig. G-9 (Continued)
Fig. G-9 (Continued)
Fig. G-10. Percent loss on ignition of the top 5 cm of soil along transects I-1.1 and I-2.1. These values are considered good estimates of percent organic matter of the soil samples examined.
Fig. G-10 (Continued)