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ECOLOGY OF WATER-LEVEL MANIPULATIONS ON A NORTHERN MARSH[1]

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INTRODUCTION

In recent years the deliberate drawdown technique has become widely used for managing waterfowl and muskrat marshes (Addy and MacNamara 1948, Uhler 1956). The Agassiz National Refuge in northwestern Minnesota has been the scene of an extensive program of this type. Here, following the original flooding in 1939 and 1940, large areas of open water had been created by the gradual disappearance of emergent vegetation, although some beds of hard-stem bulrush and reed persisted in the middle of two pools where mineral soil was present. The destruction of these emergent marshes reduced nesting habitat for diving ducks; waterfowl brood and moulting cover; favorable muskrat habitat; and had exposed the dikes to greater erosion by wave action.

A program of water-level manipulations to establish emergent vegetation was conducted in this area between 1949 and 1957. This planned program of drawdowns, with the revegetation of open-water areas as the primary objective, resulted from observations of the invasion by emergents and annual weeds of mud flats formed in 1949 and 1951 when two pools were drained to allow dike repairs.

During the growing seasons of 1953 and 1954, the senior author made an intensive study of the ecological changes associated with these drawdowns (Harris 1957). Refuge personnel cooperated in extending the work through the 1955, 1956, and 1957 seasons. Throughout this report the term "drawdown" applies to the reduction of water levels for 1 or more years, and the restoration of levels is termed "reflooding."

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A survey of the literature shows that various authors have mentioned the detrimental effects that prolonged stabilized water levels have on most species of emergent aquatics (Uhler 1944, Penfound and Schneidau 1945, Sharp 1951, Martin 1953, McDonald 1955). Other workers have pointed out that drawdown operations are useful in the production and utilization of crops of annual food plants such as millets and smartweeds (Bellrose 1941, Pirnie 1941, Griffith 1948, Schmidt 1951, Crail 1951). Stearns, MacCreany, and Daigh (1940) and Cottam and Bourn (1952) have discussed plant succession on drained lakes. Lynch, O'Niel, and Lay (1947), McLeod (1949), Baldwin (1950), and Martin (1953) all have mentioned that many emergent aquatics require bare mud flats for successful germination and seedling establishment. The use of the drawdown technique in a planned program of perennial emergent management has been discussed by Errington (1948), Schmidt (1953), Nelson (1954, 1955), and Uhler (1956). Recently Kadlec (1962) has reported in detail on a drawdown carried out in 1958 by the Michigan Department of Conservation.

THE STUDY AREA

The Agassiz National Wildlife Refuge lies in the ecotone between the grassland and coniferous forest in northwestern Minnesota. The more than 60,000 acres of the refuge vary only about 20 feet in elevation. The mineral soil, a slightly alkaline clay-sand, is overlain in many places with considerable peat. Much original peat was removed by fire when the entire region was drained and farmed between 1911 and 1937 (Hunt and Mangus 1954). In some parts of the refuge, the bare mineral soil is now exposed; in other parts the present soil type is peat ash, partially decomposed peat, silt, or unburned peat. The marsh area approximates 25,000 acres in 14 artificial pools.

The open-water areas of the pools support beds of submerged vegetation that include white-water crowfoot (*Ranunculus trichophyllus*), cursed crowfoot (*R. sceleratus*), sago (*Potamogeton pectinatus*), red-head pondweed (*P. Richardsonii*), pondweed (*P. pusillus*), water milfoil (*Myriophyllum exalbescens*), and coontail (*Ceratophyllum demersum*).[2] In midsummer filamentous green algae, lesser duckweed (*Lemna minor*), and star duckweed (*L. trisulca*) often form a heavy scum on the surface of open-water areas.

Inshore the open-water areas give way to emergent marshes consisting of one or more of the following: common cattail (*Typha latifolia*), narrow-leaved cattail (*T. angustifolia*), a variable cattail suspected of being a hybrid between common and narrow-leaved cattails which resulted from the drawdown operations, soft-stem bulrush (*Scirpus validus*), hard-stem bulrush (*S. acutus*), river bulrush (*S. fluviatilis*), creeping spike-rush (*Eleocharis palustris*), reed (*Phragmites communis*), giant burreed (*Sparganium eurycarpum*), and three "marsh sedges" (*Carex atherodes, C. Pseudo-Cyperus,* and *C. lacustris*).

Shoreline moist-soil areas are dominated by cattails, reed, sedges, and upland weeds such as mint (*Mentha arvensis*), water horehound (*Lycopus americanus*), and bedstraw (*Galium* spp.).

Methods

A wide variety of conditions was available for this study. Seven pools were drawn down and the bottom of an eighth was exposed during the abnormally dry summers of 1952 and 1953. The result was the establishment of emergent vegetation on some 5,000 acres of the approximately 12,000 acres of previously open water. Portions of the bottoms of the pools were exposed for two growing seasons. Water levels were lower during the second year than the first and, in each season, gradually declined. Thus within any single pool it was possible to select areas that had been exposed at variable intervals ranging from two complete growing seasons to only a few weeks. One pool was drawn down 4 years and partially reflooded the following year, so that certain contours provided opportunity for observations on a fifth year of exposure.

Circular 1/100-acre study plots were established at 48 separate locations which were selected to represent either particular contours of the pool bottoms or stands composed of those species of major interest. The plots were located in four separate pools and collectively sampled the entire operation of pre-drawdown conditions, 5 years of drawdown, and 5 years of reflooding. During drawdown, data were obtained on 23 plots in the first year; on 24 plots in the second year; on 1 plot in the fourth year; and on 4 plots in the fifth year. After reflooding, counts were made on 48 plots in the first 3 years; on 22 plots in the fourth year; and on 14 plots in the fifth year.

Eight 1-square-foot subplots were established within each study plot to determine species composition, density, and growth. The subplots were located mechanically, two in each cardinal compass direction from the center stake of the circular plot. All stems in the subplots were recorded. With high densities of seedlings or small plants, such as needle rush (*Eleocharis acicularis*), counts were made only in the upper left square decimeter of each subplot and later converted to stems per square foot. In addition to these intensive studies, general observations of plant occurrence were made on all pools.

Densities of submergents were classified by visual subjective estimates into one of four groups: trace, light, medium, and heavy. Details of methodology and plot data are recorded in Harris (1957).

[2] Botanical nomenclature follows Fernald (1950).

Results

Most open-water areas were poorly vegetated with submerged aquatics prior to drawdown, and these plants had little effect on the establishment of vegetation after exposure. Growths of filamentous green algae sometimes formed thick mats that dried to a tough leathery texture upon exposure. Germination underneath this mat was retarded and seedlings usually could not penetrate it.

First year of drawdown

Five vegetation types developed during the first year of drawdown (Table I, Fig. 1). These marshes were classified as follows: (1) emergent; (2) emergent-fleabane; (3) fleabane; (4) emergent-mud flat weed; and (5) mud flat weed.

Emergent marshes.—Emergent marshes ranged from pure stands of soft-stem bulrush, through various mixtures, to nearly pure stands of cattails. Differences in composition from place to place seemed to be determined by the time of drawdown, availability of seed, and soil type. Emergent stands were favored by early June drawdowns on silts rich in organic material that dried slowly (Fig. 1). The seeds of these emergents were available in various ways. Cattail seed blew onto the flats in unlimited amounts from thousands of acres of shoreline cattail stands. Residual seed in the soil produced widespread stands of bulrush.

TABLE I. General types of vegetation that developed during the first year of drawdown

Type of marsh	Approximate species composition	Density range (stems/sq ft)[1]	Time of exposure	Approximate rate of superficial drainage	Soil type	Amount of algal debris
Emergent	Soft-stem bulrush and cattail dominate; burreed, spike-rush and sedge understory; variable dominance, from pure bulrush to pure cattail	5 to 10 in cattail stands; 50 to 65 in bulrush stands (16)	Early to mid-June	Slow (10-15 days)	Silts and peats	None
Emergent-fleabane	Co-dominance of fleabane and various emergents; 50-75% fleabane and 20-40% emergents	15 to 35 (24)	Mid-June to early July	Very slow to slow (10-20 days)	Silts and peats	None to light
Fleabane	Pure fleabane except for trace amounts of other species	30 to 55 (16)	Early July	Very slow (15-20 days)	Peat-silts and peats	Variable, usually none
Emergent-mud flat weed	Various mixtures of fleabane, coast-blite, emergents and dock; no dominance by any single group	Variable, 2 to 70; most on early areas, least on latest areas; most areas about 15 to 20 (80)	July 10 to early August	Moderate (7-10 days)	Variable	Variable
Mud flat weed	Mixtures of dock, coast-blite, and fleabane with traces of cattail	5 to 15 (16)	Mid-summer	Rapid (3-5 days)	Coarse alkaline silts	Heavy

[1] Numbers in parentheses are the number of square feet in each sample.

Buoyant seeds of giant burreed were often windrowed around the edges of pools, on dikes and ditch banks, and in shallow water areas.

Emergent-fleabane marshes.—In 1952 for the first time, marsh fleabane (*Senecio congestus*) assumed a co-dominant role with soft-stem bulrush, cattail, and creeping spike-rush over considerable areas of mud flats. The life cycle of marsh fleabane begins in early July when ripe seed is disseminated by wind. Germination, seedling establishment, and seedling development follow rapidly after the seed falls onto a wet mud flat. By fall root systems are well-developed and the leaves form rosettes 2-6 inches in diameter. The plants lie dormant during the winter. Between May 1 and July 1 the rosettes develop into bulky plants 36 to 50 or more inches tall, each of which may occupy as much as a square foot of ground. Blooming reaches a peak in late June and after seed dissemination in early July, the old stalks die.

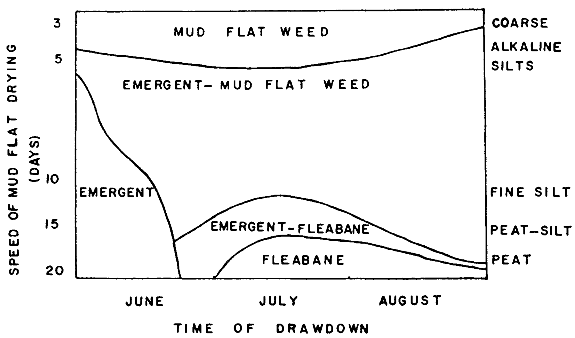

FIG. 1. Schematic presentation of the development of five major vegetation types during the first year of drawdown in relation to time of drawdown, rapidity of drying of mud flat, and soil type.

During the early years emergent marshes were most common in response to June and early July drawdowns, whereas emergent-fleabane marshes were common after 1952. The explanation for this change seems to be fleabane seed availability. Prior to 1948 the water levels of the pools had been relatively stable, and little mud flat acreage was available to fleabane colonization. As a result, the total fleabane population on the refuge at that time must have been small. Although no records of fleabane abundance are available prior to 1952, presumably the species persisted during the non-drawdown years in patches along ditch banks and pool edges that were exposed each year by evaporation. As the area of mud flat exposed by drawdown increased from year to year, the fleabane population probably increased gradually until the summer of 1952 when enough seed was produced to colonize all available mud flats. Prior to 1952 fleabane was unknown to Refuge personnel. After that time fleabane was a major component of the vegetation on the drawdown areas.

The emergent-fleabane type developed on peat-silts which were exposed initially in mid-June but which dried slowly and thus were still wet in early July. Causes of slow drying were low evaporation rate, slow rate of drainage, rain, and wind seiche. Usually cattail and bulrush seedlings appeared by late June in scattered amounts, and the bare areas of the mud flats were colonized rapidly by fleabane as seed became available in July.

Fleabane marshes.—Typical fleabane stands developed on peats and peat-silts that were very slowly exposed in early July. Fleabane seed dispersal was at its peak at this time and the wet peat soils provided ideal germination surfaces. Under such conditions fleabane often attained densities of 55 stems/sq ft in 50-60 days and formed a lawn-like mat which crowded out all other plants. Pure fleabane stands occasionally became established on areas initially exposed as late as early August when weather conditions and rates of drawdown prevented a rapid drying of the mud flat and when seed was available from nearby decaying stands of mature fleabane. Such conditions were atypical and uncommon.

Emergent-mud flat weed marshes.—Many areas developed into various mixtures of marsh fleabane, coast-blite (*Chenopodium rubrum*), creeping spike-rush, cattails, soft-stem bulrush, marsh sedges, and dock (*Rumex maritimus*) without dominance by a single species. This vegetation type was widespread on midsummer drawdown areas that dried moderately rapidly (Table I). On these areas cattail and soft-stem bulrush seedlings appeared in the more moist regions within 10 days after exposure. Coast-blite appeared in the first 2 weeks and, as the flats dried, this plant prospered and dominated. In the fall the general appearance was one of a moderate stand of cattails about 2 feet high with an understory of coast-blite and lightly intermixed with soft-stem bulrush, marsh sedge, creeping spike-rush, and various weeds such as dock, stick-tight (*Bidens* spp.), sedge (*Carex sychnocephala*), marsh fleabane, and smartweed (*Polygonum* spp.). In general, the later the exposure, the less dense the vegetation which became established.

Several factors interacted to determine the exact composition and density of any individual stand. Generally, the more an area combined early season drawdown, peat-silt soils, slow drying of the mud flats, and small amounts of stranded algal debris, the greater was the tendency for the development of emergent aquatics. Any deviation from these environmental conditions increased the importance of mud flat weeds. In the shallows of sheltered pools which dried relatively rapidly the emergent component was almost exclusively marsh sedge. Apparently this condition was dependent on the ability of marsh sedge seedlings to become established on dry soils and on marsh sedge seed availability. The buoyant seeds of these *Carex* species are pushed by wind action to the edges of the open-water areas where they await favorable germination conditions.

Mud flat weed marshes.—Coast-blite, dock, and marsh fleabane developed in areas where coarse alkaline silts with heavy mats of algal debris were rapidly exposed in mid- and late summer. There was a nearly complete absence of emergents. On these areas coast-blite was the first plant to appear after drawdown, becoming established quickly and attaining maturity during August and September. In late September marsh fleabane and dock predominated, and cattail was usually present only in trace amounts.

Second year of drawdown

Moyle and Nielsen (1953) point out: "The rapidity of drainage and the physical and chemical changes of the soils accompanying drainage, vitally affect plant invasion and succession. This may be contrasted to the classical concept of plant succession whereby the plants themselves gradually change the habitat from the xeric or hydric to a mesic state." These workers found a telescoping, general acceleration, and often a lack of orderly succession, in the normal successional seres which were expected on the drained basins of several northern Minnesota lakes.

The five vegetation types of the first year varied considerably in their reaction to a second year of exposure (Table II). Some areas progressed rapidly along "classic" lines of plant succession toward upland communities similar to the telescoping and general acceleration observed by Moyle and Nielsen (1953). Other areas, which had been initially dominated by some emergent species, showed little tendency to progress toward upland communities in 2 years of exposure. Environmental factors contributing to this variation were the density and composition of the residual vegetation, the soil type, and soil-moisture conditions during the second year.

Emergent marshes.—Two general lines of development took place. In the first, dense first-year stands on fine silts and peat-silts with favorable soil-moisture conditions in the second year continued their development into very dense emergent marshes. All such cases were pure soft-stem bulrush marshes on areas which had been exposed initially during late May and early June of the first year. This development is similar to that found by Wilde, Youngberg, and Hovind (1950) who pointed out that the persistence of marsh emergents in the succession following drainage of beaver ponds in Wisconsin was determined largely by the nature of the substrata. Peat and rich

TABLE II. General summary of changes in vegetation between first and second years of drawdown

Type of stand at end of first year	Major changes in second year	Contributing Environmental Factors: Soil moisture	Soil type	Amount of competition by residual vegetation	Type of stand at end of second year
Emergent	1. Bulrush stands-increase	Favorable	Silts and peat-silts	Bulrush prevents growth of others	Emergent
	2. Cattail stands-closed with weeds	Moderate fast drying	Coarser silts	Not severe	Emergent-weed
Emergent-fleabane and fleabane	Near-elimination of residual vegetation except fleabane; invasion of upland and shore-line weeds in late summer	Complete superficial drainage by July	Silts and peat-silts	Severe	Weed
Emergent-mud flat weed	1. Emergents reduced; shift from mud flat to upland weeds	Complete drying; high contours	Silts	Severe	Emergent-weed
	2. Emergents-no change; shift toward upland weeds	Moderate drying mid-contours	Silts	Moderate	Emergent-weed
	3. Increase in emergents and mud flat weeds	Favorable; low contours	Silts	Little	Emergent-mud flat weed
Mud flat weed	Sparse cover of mud flat and upland weeds with some cattail	Complete drying	Coarse silts	Little	Emergent-weed

muck soils where soil drainage was slow retained sedges (the initial invaders on their areas) for several decades, resisting invasion of upland woody species.

The second type of development took place in stands of cattails which were partially closed at the end of the first year of drawdown and which grew on coarser soils where the superficial soil layers had dried more completely during the second year. No cases of completely closed pure stands of cattails were observed after 1 year of drawdown. Cave-Brown-Cave (1948) and Summerhayes and Turrill (1948) also reported that dense stands of cattails were still being closed by seedlings of cattail, willow, and upland mosses more than 1 year after drainage of a lake in England. Such partially closed cattail stands at Agassiz Refuge developed into mixtures of emergents, mud flat weeds, and upland weeds such as Canada thistle (*Cirsium arvense*), field sow thistle (*Sonchus arvensis*), willows (*Salix* spp.), and sweet clover (*Melilotus* spp.) in more or less equal proportions during the second season. There was a distinct tendency toward upland plant communities, and at the end of the second year the marshes had changed to an emergent-weed condition.

Emergent-fleabane marshes.—Emergent-fleabane stands developed into dense stands of fleabane during early summer of the second season. Fleabane provided intense competition to the emergents. After mid-July, when fleabane growth was completed, soil drainage had progressed to the point where the surface was no longer favorable for emergent seedling establishment. In most cases density of all vegetation was reduced during the second year, the only notable exception being creeping spike-rush. The increased density of spike-rush was largely the result of expanding vegetative growth by individual clumps that had become established during the first year.

Fleabane marshes.—Stands of fleabane completed their development during the early summer of the second year and prevented the establishment or growth of emergent vegetation. By the time fleabane growth was completed, soil drainage and evaporation had dried the substratum sufficiently so that little new vegetation became established. The vegetation which persisted was composed almost entirely of various weeds.

Emergent-mud flat weed marshes.—The various emergent-mud flat weed areas developed along three general lines during the second year of exposure. Important controlling factors were residual vegetation densities, fleabane growth, and drying of surface soil layers.

The first line of development was exhibited by stands which were dense and almost closed at the beginning of the second season. Usually fleabane made up an appreciable part of this vegetation. General competition from the high residual density, the maturing fleabane, and the drying of the surface soil during the summer caused an overall reduction in the density of the total as well as of the emergent vegetation on such areas. They became emergent-weed marshes at the end of the second year of drawdown. Differences between these and first-year marshes on the same areas were a reduction in the emergent vegetation and a shift from mud flat species towards upland weed species.

The second line of development concerned partially-closed residual stands of moderate density with moderate amounts of fleabane. Competition afforded during early summer did not serve to reduce the overall density of vegetation or of emergents. The two most conspicuous changes that occurred were a greater proportion of upland weed species and a noticeable increase in willow.

A third line of development took place in residual stands of light density that had become established as a result of late first-season drawdown. Such areas usually were located on low contours of the pool areas and thus were only superficially drained at the beginning of the second year. Fleabane densities were light. Favorable soil moisture and a lack of important competition from residual vegetation presented a mud flat during the early spring of the second season that was similar to a first-year drawdown initially exposed in early summer. Vegetation development likewise was similar to that of the first-year drawdown. At the end of the second season of drawdown a typical emergent-mud flat weed marsh dominated by cattail, soft-stem bulrush, coast-blite, and marsh fleabane was present. Emergent species were better represented than on most midsummer emergent-mud flat weed areas.

Mud flat weed marshes.—Mud flat weed marshes began their second year without a great deal of residual vegetation because most of the mud flat species were spring and summer annuals which matured at the end of the first year of drawdown. The prevailing conditions duplicated those of a first-year early summer drawdown on well drained soils. By the end of the second year such areas supported a sparse cover of mud flat and upland weeds intermixed with a moderate amount of cattail.

Third, fourth, and fifth years of drawdown

A single pool was drawn down for 5 years. General observations were made during these years, and some plot data were collected in the fourth and fifth years.

Spring runoff was not completely drained from the pool basin until sometime in June of the third year. Continued soil drainage during the summer resulted in a firm and dry pool bottom by fall. Mud flat annuals such as coast-blite, stick-tight, and smartweeds thrived, and emergent species, although well represented, were not present in dense stands.

During the fourth year the summer was very dry and the bottom became thoroughly dried out and solid underfoot. The emergent aquatics did not thrive in the face of these low moisture conditions and severe competition from upland weed species. The dominant plants were artificially seeded Japanese millet, coast-blite, sweet clover, sow thistle, smartweed, willow, and Canada thistle. Emergents were present.

Willow became particularly noticeable. In the fall the pool was dry and looked like a field overgrown with willows about 3 feet high. Areas located on the lower contours where soil drainage was not as complete developed into patches of marsh sedge, sprangle-top (*Scolochloa festucacea*), or mixtures of marsh sedge, cattails, and soft-stem bulrush. These patches appeared as islands of meadow in a low brushy "jungle."

The pool was to have been reflooded in the fifth year. However, the extremely dry bottom, light runoff, and a second successive dry summer allowed only a few inches of water to accumulate. As a consequence, many portions of the pool bottom were exposed for a fifth year. In these areas rapid growth of willow occurred. Plants that had been 24-30 inches high in June reached 60-72 inches by fall. In June individual roots were represented by only single or double stems, but by September clumps of five to ten stems completely covered areas of over 3 square feet each. Possibly a contributing factor to this lush willow growth was more favorable soil moisture conditions resulting from the partial reflooding of the pool bottom. Aspen (*Populus* spp.) saplings became conspicuous. In spite of the severe competition of the willows, the various emergents still persisted in favorable locations and annual upland weeds were lightly represented.

Effects of reflooding on vegetation

Regardless of the type of vegetation present at the end of drawdown, cattail, soft-stem bulrush, spike-rush, marsh sedge, willow, and a few moist soil species such as sprangle-top and reed-canary grass (*Phalaris arundinacea*) accounted for most of the vegetation which grew after reflooding. Aquatic annuals such as sloughgrass (*Beckmannia syzigachne*) developed in small quantities on a few areas. Spring and summer mud-flat, shoreline, and upland annuals completely disappeared.

The exact type of marsh that first developed after reflooding depended both on the composition and density of the residual vegetation and on the depth of the restored water. These results are similar to those described by McLeod (1949). The growth of nearly pure stands of soft-stem bulrush and marsh sedge was limited to localized areas that had developed such stands during drawdown. These stands usually were quite dense regardless of water depths and often had a moderate understory of creeping spike-rush. Both the spike-rush and the bulrush developed a heavy seed crop, while the seed crop on the sedge was negligible.

Creeping spike-rush, usually present as an understory in other types of emergent marshes, occasionally developed either nearly pure but patchy stands of light density without any important competitors, or stands of substantial densities which were overtopped by a light scattering of other emergents but in which spike-rush was still clearly the dominant. In the first case, the light patchy stands developed on former emergent-fleabane areas which had a history of 2 years of drawdown. Other emergents were nearly absent as a result of competition with maturing fleabane. In the second case, the mixtures of dense spike-rush and light scatterings of other emergents developed on former emergent-weed areas where a fairly dense stand of mixed emergents had developed during the first year of drawdown and that had been drawn down a second year. As previously stated, in the second year of drawdown on such areas, general competition, fleabane competition, and drying of the mud flats reduced the emergent vegetation, resulting in a greater loss of cattail and bulrush than of spike-rush.

Areas with a history of very rapid rates of drying, heavy mats of dried algal debris, stands of pure fleabane, or a combination of these factors failed to develop any emergent vegetation after reflooding and became areas of open water with some submergents.

Areas which had been drawn down for 4 and 5 years continued to be dominated by willows following reflooding. Willow was the only important non-aquatic plant present after reflooding on any area.

Cattail stands, containing a light mixture of other emergents, were widespread over most areas exposed during the summer where environmental conditions of drawdown had not been favorable enough for bulrush, harsh enough for spike-rush or marsh sedge, or prolonged enough for willow. The cattails were of two distinct types: (1) common cattail, which developed in certain areas and was rather intolerant to reflooding; and (2) a variable form resembling *Typha glauca* but suspected to be a hybrid between common cattail and narrow-leaved cattail. This form is referred to here as "hybrid" cattail, is quite tolerant to flooding, is very thrifty, and developed in great quantity.

Although the density and composition of the individual stands after reflooding varied greatly, the overall density showed a positive relationship to the position of the stand on the pool contour, the deeper areas having the sparsest stands (Fig. 2). Stands that developed on coarse alkaline soils

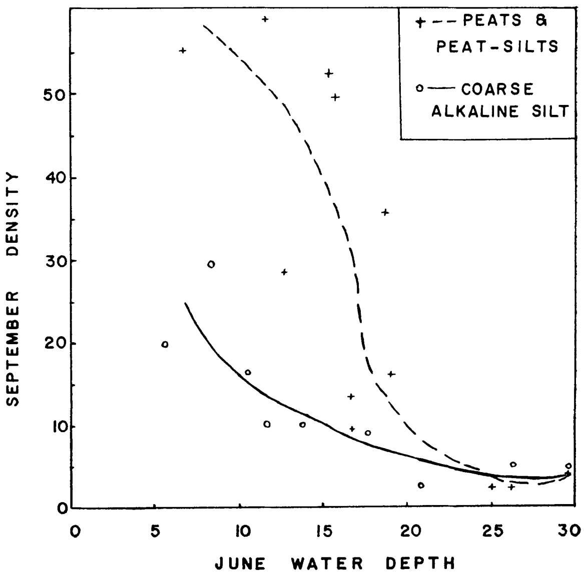

FIG. 2. General relationships between fall vegetation density (stems per square foot) in first year of reflooding, early summer water depth (inches), and soil type.

were generally less dense than those on fine organic soils. Several interrelated factors contributed to this contour-density relationship: (1) at the time of the initial drawdown, the stands on the lower pool contours were exposed later in the season when conditions were less favorable for emergents in contrast with the favorable situation of the higher-early exposed contours; (2) the lower contours were exposed for a shorter total time, thus giving any emergents that did develop less time for vegetative growth and less opportunity to become well rooted and firmly established (generally true of 1-year-drawdown areas); and (3) lower contours were reflooded to a greater depth, which undoubtedly prevented optimum growth on these areas during the first year of reflooding.

During subsequent years of reflooding, emergents generally disappeared from the new marshes. The rate of disappearance was dependent on the species present and on water depths (Table III). Data on the total number of stems of all species in all plots were grouped according to the average water depth after reflooding. The total number of stems present in each year of reflooding was

TABLE III. Survival indices for emergent species in four years of reflooding on study plots

Species	Year of reflooding	Summer Water Depth (in.) 0-10	11-15	Over 15
Scirpus validus	1	100	100	100
	2	50	31	26
	3	19	15	Trace
	4	3	0	0
Square feet in sample		32	32	120
Total stems first year		307	102	854
Eleocharis palustris	1	100	100	100
	2	46	83	27
	3	19	17	0
	4	1	0	0
Square feet in sample		24	40	120
Total stems first year		247	240	1536
Marsh sedge	1	100	100	100
	2	280	91	85
	3	270	18	19
	4	220	0	0
Square feet in sample		32	40	104
Total stems first year		32	264	457
Typha spp.[1] (mostly hybrid)	1	100	100	100
	2	120	92	85
	3	134	83	88
	4	167	108	58
Square feet in sample		32	40	96
Total stems first year		48	96	74

[1] Reductions in cattail due almost entirely to loss of *T. latifolia* and not "hybrid".

then expressed as an index using the number present in the first year as a base of 100. An index greater than 100 in subsequent years indicates that the species increased in density, while an index less than 100 indicates a reduction in density (Table III).

Following are detailed notes on the response to reflooding of the five major plant species found on reflooded areas. In each case observations cover a 5-year period.

Scirpus validus

Soft-stem bulrush died out of the marshes rapidly during the second year when flooded with over 15 inches of water. This condition was also reported by Sharp (1951) who stated that a community made up of wild rice (*Zizania aquatica*), duck potato (*Sagittaria* spp.), and soft-stem bulrush "may persist for years . . . on rich soil types . . . provided that water levels during the growing season do not exceed 15 inches during June and recede during July and August to a few inches. . . ." The destruction of soft-stem bulrush was essentially complete at Agassiz Refuge in over 15 inches of water in 3 years and in any continuously flooded area in 4 years.

First year: Developed in approximate proportion to its occurrence at the end of the drawdown. Heavy seed crop. Good development after both 1 and 2 years of drawdown in water from 6 to 24 inches.

Second year: Began to die out. Slight to moderate density reduction in less than 12 inches of water; marked loss in 15 to 24 inches. Good seed crop in all depths on plants that survived.

Third year: Complete elimination in depths from 15 to 24 inches. Although still persisting in light densities, largely replaced by cattail in most shallow depths.

Fourth year: No growth in areas continuously reflooded to any depth. Present only in trace amounts in shoreline evaporation "tension" zones where it is being replaced by cattail.

Fifth year: No growth in areas continuously reflooded to any depth. Entirely replaced by cattail in shoreline evaporation zones.

Eleocharis palustris

Creeping spike-rush also died out of the marshes rapidly during the second year when flooded with over 15 inches of water. Gates (1948), however, recorded the persistence and progressive colonization of creeping spike-rush on an open shoal in shallower water depths of approximately 12 inches over a period of 20 years.

First year: Developed in approximate proportion to its occurrence at the end of the drawdown. Grew in nearly pure stands on some areas where moderately harsh environmental conditions prevailed during drawdown. Understory to other emergents on most areas. Good seed crop.

Second year: Marked reduction in water over 20 inches deep. Slight to moderate increase in shallow depths of former emergent-fleabane areas drawn down 2 years which lacked important competition from other emergents. Little change in density in less than 15 inches where overstories occurred. Good seed crop.

Third year: Complete or near-complete elimination in depths over 20 inches. Present only as remnant stands in shallow depths with emergent overstories. Increased in shallow areas where heavy willow overstory began to die. Good seed crop.

Fourth year: No growth in water over 15 inches deep. Occurred only in trace amounts in some shallow areas. Completely eliminated in most shallow areas. Still present in shore line "tension" zones in light amounts.

Fifth year: No growth in areas continuously reflooded to any depth. Still present in shoreline "tension" zones.

Typha spp. (*T. latifolia* and hybrid)

Common cattail was greatly reduced during the third year of reflooding in over 12-15 inches of water and was completely eliminated in such depths during the fourth year (Table III). Uhler (1944), Moyle and Hotchkiss (1945), Penfound and Schneidau (1945), Errington (1948), Sharp (1951), and Martin (1953) have all reported that cattails die out of marshes if they are continuously flooded to depths ranging from 1 to 4 feet. McDonald (1955) noted that common cattail is least tolerant of deep waters, that *T. glauca* is more tolerant, and that narrow-leaved cattail is most tolerant. McLeod (1948, 1949) stated that following initial flooding emergent vegetation reaches a maximum in 2 or 3 years, degenerates in 4 or 5, and is gone in 10, and that this process can be speeded by increased wave action and water levels. In contrast to other emergents, the hybrid cattail showed little tendency to die out in water up to 24 inches deep with 4 years of reflooding (Table III). By encroaching on openings created by the death of other species or into openings that had never been vegetated, hybrid cattail threatened to become a problem species.

First year: Developed in approximate proportion to its occurrence at the end of the drawdown. None to very light seed crop. Good growth in all depths.

Second year: Heavy increases in plant size and densities in less than 12 inches of water. Some destruction of typical common cattail in over 18 inches. Heavy growth of hybrid in depths up to 24 inches and good growth in greater depths. Moderate seed crop.

Third year: Heavy death of common cattail in over 18 inches. Excellent survival and growth of hybrid in up to 24 inches. Good seed on hybrid.

Fourth year: Complete death of common cattail in over 18 inches. Marked loss in areas normally flooded with 12 to 15 inches but flooded with 20 inches in June of each year. Good survival, growth, and fruiting of hybrid in up to 24 inches.

Fifth year: Complete death of common cattail stands continuously flooded to any depth. Good survival of common cattail in areas flooded in June to not more than 10 inches and evaporating to moist soil by August. Little data for hybrid; two light stands remained unchanged through 5 years of flooding with 20-24 inches. Little fruiting in the fifth year. No data on hybrid for shallower areas.

Carex atherodes, C. lacustris, C. Pseudo-Cyperus

Marsh sedge was greatly reduced during the third year of reflooding in over 12-15 inches of water and was almost completely eliminated at these depths during the fourth year.

First year: Developed in approximate proportion to its occurrence at the end of drawdown. Tended to dominate on sheltered areas where environmental conditions during drawdown had been moderately harsh. Best development in less than 15 inches of water. Poor seed crop.

Second year: Moderate to dense stands in up to 24 inches. No significant change from previous year. Moderate seed crop.

Third year: Marked reduction in over 12 inches. Slight to moderate reduction in shallower depths.

Fourth year: Near-complete elimination in over 15 inches. Only traces remain in over 12 inches. Most areas continuously flooded to more than 6 inches have lost all sedge. Persists on most evaporation "tension" zones.

Fifth year: No data.

Salix spp.[3]

The willows that had developed on areas drawn down 1 and 2 years died after 2 or 3 years of moderately deep reflooding without creating any serious problem of competition or debris accumulation. On areas that had been drawn down for 4 and 5 years, the willows survived and even thrived after 3 years of reflooding to a depth of less than 12 inches. In deeper areas, the top foliage began to die during the second year of reflooding and the stands exhibited partial death after 3 years of reflooding with more than 10 inches. Almost complete death occurred in the fourth year in over 10 inches. Complete death occurred after 4 years in more than 24 inches and after 5 years in 18 inches, but a great deal of woody debris remained in the marsh. Specific reactions of willows to reflooding varied according to the number of years of drawdown.

First year: No development after 1 year of drawdown. Widespread after 2 years of drawdown. Total growth at end of the first year of reflooding about 3 feet, showing distress where flooded with more than 10 inches of water. Heavy growth after 4 and 5 years of drawdown in all depths, no distress apparent.

Second year: Moderate to heavy death in 2-year-drawdown areas flooded to more than 10 inches. Thinning in tops and slight death in 4- to 5-year-drawdown areas and flooded to more than 10 inches.

Third year: Heavy to complete death in areas exposed 2 years and flooded to more than 10 inches. Slight to moderate death in 4- to 5-year-drawdown areas and flooded to more than 10 inches. Good survival in shallower depths on stands exposed 4 and 5 years.

Fourth year: Complete death in all areas exposed 2 years and flooded continuously to any depth. Complete death in areas exposed 4 years and flooded with 24 inches, and heavy death in areas exposed 5 years and flooded with 10 inches.

Fifth year: Complete death in all areas exposed 4 and 5 years and flooded with more than 18 inches. No data for shallower depths.

Effect of drawdown on submerged aquatics

Prior to the drawdown, submergent beds in most pools consisted of water milfoil and coontail with occasional beds of sago and other pondweeds in localized areas. Seed production had not been outstanding for most years.

For the period of the drawdown submerged aquatics were eliminated on the exposed areas. In pools where some areas did not dry up during the drawdown, the submerged aquatics thrived and produced heavy-to-excellent seed crops during the period of lowered water levels. The number and size of sago beds increased markedly in the unexposed portions of one pool during both years of the drawdown. Seed crops were excellent both in this species and red-head pondweed.

Although submergent growth in the lowered pools was more luxurious than previously, it was difficult to assign the increase directly to the drawdown. The summers when most areas were exposed were drier than normal, and the water levels

[3] Ten species of willow have been identified from this area (Hunt and Mangus 1954).

were lowered considerably by evaporation alone. Much mention has been made in the literature of the fact that pondweeds fruit especially well during drought summers (Muenscher 1936, Sharp 1951). Reasons for this increase during periods of lowered water levels are not thoroughly understood. Muenscher (1936) pointed out: "It cannot be assumed, as had been done by some, that fruiting induced by lowering the water was necessarily due to a change which increased the chances for wind pollination. Lowering the water level may modify various other factors such as temperature, light intensity, rate of photosynthesis, and growth, any of which may increase the possibility of fruit production." Lowering water levels also could affect turbidity, the importance of which in the growth of submerged aquatics has been pointed out by various authors (Chamberlain 1948).

The ability of submergent seeds to withstand extended periods of drying and germinate and establish beds after reflooding is well documented (Oborn 1938, Sharp 1939, Steenis 1939, Sharp 1951). At Agassiz Refuge, spectacular growth and fruiting of sago occurred in the open-water areas during the first year of reflooding. This was recorded in three different calendar years on the study plots in four different pools and was confirmed by general observations in four other pools. In the second year of reflooding sago produced moderate to heavy seed crops but the luxurious growths were not as widespread as in the first year. In the third and fourth years, submergent growth was light to moderate and the stands were dominated by coontail and duckweeds rather than pondweeds.

Discussion

The drawdown of former open-water areas at Agassiz Refuge from 1 to 5 years resulted in a variety of vegetation types. This variety was the result of one or more environmental factors, the most important of which were soil type, season of drawdown, speed of superficial drainage, speed with which the surface soil layers dried, evaporation rates, available seed, and competition of residual vegetation during subsequent years of exposure. The pattern of succession on Agassiz Refuge drawdown areas was from a mixture of annual weeds and perennial emergents through mixtures of annuals, perennials, and woody species to a community dominated by woody species after 5 years. This development is parallel to that reported by Bourn and Cottam (1950), Schmidt (1951), and Moyle and Nielsen (1953).

Because the use of drawdown techniques has possible detrimental as well as desirable effects on waterfowl marshes the duration of exposure must be limited to the minimum period necessary to accomplish the purpose for which the drawdown was conducted. The management objective in the present program was the establishment of perennial emergent vegetation in former open-water areas. In areas exposed for more than 2 years, natural succession toward upland communities proved to be so rapid that drawdowns for longer periods were undesirable.

A comparison of 1- and 2-year-drawdown areas reveals that, in general, during the first year of drawdown, areas of early initial exposure developed moderately dense stands of emergents while those exposed after the first of August developed sparse stands. During the second year of exposure areas with high densities during the first year lost much vegetation, and those with low densities developed a second-year vegetation of considerable density (Fig. 3). This inverse relationship between first- and second-year densities on a given area is complicated by the speed with which the superficial soil layers dried during the second year. Providing soil types are similar, the earlier the time of initial drawdown, the greater the amount of drying the second year. The areas exposed later are at lower pool contours and pre-

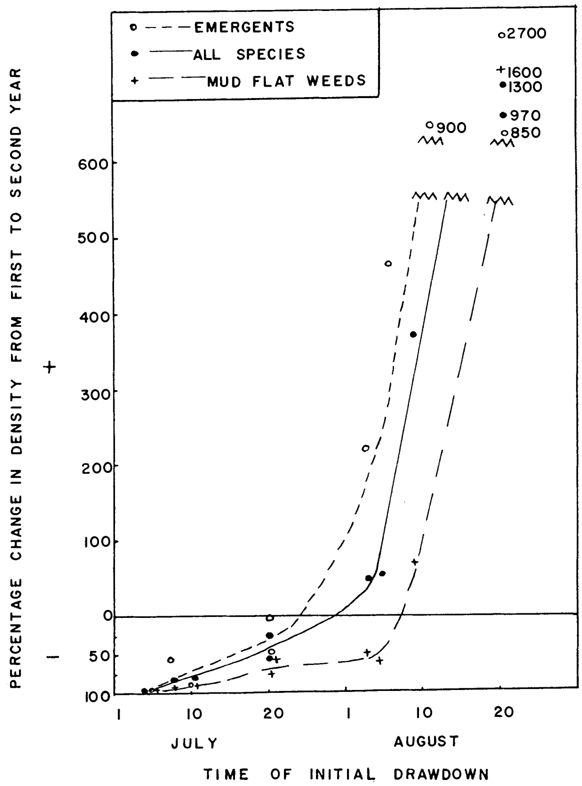

FIG. 3. Percentage change in stem density on study plots between first and second years of drawdown.

sumably are nearer the underground water table, and thus do not dry out as thoroughly the second year. In every case where these stands lost vegetation in the second year, it seemed to be caused by unfavorable soil moisture conditions in mid- and late summer coupled with severe competition in early summer resulting either from dense fleabane stands or from high residual densities of other species.

In most cases, properly handled 1-year drawdowns were more successful in establishing stands of the desired emergents than 2-year drawdowns. Two methods of 1-year drawdown could be employed: (1) an early summer drawdown in which superficial drainage is completed no later than June 15; or (2) a late summer or early fall drawdown in which superficial drainage is completed early the following spring.

The marshes which resulted from the drawdown were short-lived from a standpoint of waterfowl food production. Creeping spike-rush and softstem bulrush, which were the only two important seed-producing emergents that developed in quantity, died out of the marshes rapidly after reflooding. In spite of the fact that spike-rush persisted quite well in the shallower depth, this species usually was not an important seed producer because of its light density where overstories of other emergents occurred. Thus substantial waterfowl food production by emergent species on drawdown marshes occurred for only the first year of reflooding, with some occurring during the second year and almost none during the third.

Because cattails and marsh sedge, of value as cover plants, persisted longer after reflooding, the marshes lasted at least 4 years. It appears, then, that the major justification for the establishment of emergent marshes over large areas must be made on the basis of a need for emergent cover. Except for hybrid cattail, the new emergent marshes which had been reflooded to depths of more than 15 inches lost the majority of their emergent species in approximately 4-5 years after reflooding. Such areas would therefore need a new drawdown once every 5 or 6 years to maintain emergent cover. Areas flooded with less than 15 inches and vegetated with species other than hybrid cattail probably would need a drawdown once every 7 or 8 years.

The general pattern for submergents was one of heavy growth of desirable species the first year of reflooding, moderate to heavy growth in the second year, and rapid decline in growth in the third and fourth years. These changes may be the result of several different forces. Drawdowns may increase the decomposition of organic material so as to release carbonic acid which in turn precipitates colloidal clay from the water, thus allowing greater light penetration and better submergent growth (Uhler 1956). Continued flooding may lead to an accumulation of organic material which ties up the available nitrogen in the aquatic nutrient turnover since the decomposition of this material rarely progresses beyond the amino-acid state, a form not available to plant growth (McLeod 1949). On the other hand, exposure and aeration may speed this decomposition and thus release the nitrogen back into the cycle in an available form. Apparently this same process also applies to some other nutrients (Cook and Powers 1958). Kadlec (1962) discusses the complexities of these interactions.

Cook and Powers (1958) have also pointed out the possibility that, because the decomposition of organic material is slow in northern marshes and the inherent fertility low, continued marsh fertility apparently depends partially on the leaching of nutrients into the marsh from the watershed. Thus, too-frequent drawdowns or annual heavy replacement of the water in a pool during runoff may actually lead to a decline in fertility through the flushing away of nutrients which are present in the marsh ecosystem.

The drawdown operation designed to release nutrients for plant growth should endeavor to compromise these two opposing forces: (1) the release of nutrients by drawdown and decomposition; and (2) the draining-away of nutrients by drawdown and flushing. Much more study into the "nutrient turnover" in northern marshes, both artificial and natural, is required before specific consequences of artificial and natural drawdowns on soil fertility can be stated. It would seem certain, however, that at Agassiz Refuge in order to conserve any nutrients released by a drawdown, the near-complete replacement of pool waters during runoff is to be avoided in the first 2 years following a drawdown.

Many productive, natural water bodies are subjected to periods of water abundance, fluctuation, and scarcity—i.e., natural drawdowns caused by climatic changes. It seems probable that some species of aquatic plants which are regarded as desirable in marshes have developed adaptations for survival in response to these natural fluctuations, even to the point where these plants may actually require such fluctuations for continued survival and seed production. These natural fluctuations should therefore be studied and then duplicated on the artificial marshes which can be deliberately manipulated. Since the time, magnitude, frequency, nature, and consequences of the fluctuations to be used in an artificial program undoubtedly vary widely by area and management objective, these programs must be carried out only with proper study and control.

Summary

A study of vegetation changes associated with marsh drawdowns at Agassiz National Wildlife Refuge, Minnesota, revealed that the development of five types of vegetation on mud flats during the first year was influenced by seed availability, soil type and moisture, season and duration of drawdown, and the amount of stranded algal debris. The more an area combined early season drawdown, rich soil types, slow rates of mud flat drainage, and small amounts of stranded algae, the greater was the development of emergent aquatics.

In the second year of drawdown, most areas developed greater amounts of upland and shoreline weeds and fewer emergents. Areas originally exposed before August of the first year lost emergent cover during the second year, while the reverse was true of areas exposed later in the first year. Specific changes were influenced by density and composition of residual vegetation, soil types, and soil moisture. During longer drawdowns the soil dried more completely, and over a 5-year period nearly solid stands of willow developed.

Upon reflooding, mud flat and shoreline annuals were eliminated and marshes of cattails, soft-stem bulrush, sedges, spike-rush, willows, and aquatic annuals developed in the first year. Specific development in subsequent years was determined by the nature of the residual vegetation and the depth of the restored water. Spike-rush and soft-stem bulrush were destroyed by flooding with over 15 inches of water in 3 years and in any continuously flooded area in 4-5 years. These species persisted only in shoreline evaporation zones. Common cattail and sedges were gone from continuously flooded areas in 4-5 years and also persisted only in shoreline evaporation zones. "Hybrid" cattail remained unchanged in 24 inches of water throughout 5 years of flooding. Two-year-old willows died in 2-4 years in all depths, but willows on 4- to 5-year-drawdown areas were killed only where flooded with 24 inches for 3-4 years or 18 inches for 5 years.

Depending on water depths and cover types, 1- or 2-year drawdowns at 5- to 10-year intervals are required to maintain emergent marshes at this refuge. Stands of hybrid cattail may be an exception.

Sago made outstanding growth and seed production in the first year of reflooding. Significant changes in soil chemistry and nutrient availability which probably occurred during drawdown, are suspected to be a contributing factor to this growth.

Until present limited knowledge of the consequences of drawdown is enlarged, the technique should be used only for specific purposes with proper control and study.

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CONTAMINATION OF PLANT FOLIAGE WITH RADIOACTIVE FALLOUT

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Introduction

Plant foliage that has been contaminated with fallout from nuclear detonations is a major source of radioactive fission products in the diet of milk-producing livestock. Radioisotopes of strontium, iodine, cesium, and barium are absorbed from the diet of grazing animals and transferred to man via milk and dairy products (Comar, Russell, Wasserman 1957, Anderson et al. 1958, Campbell et al. 1961). Fallout lodged on plant foliage is a source of external ionizing radiation to growing plants and also a source from which certain fission products may be absorbed directly through foliage. The purpose of this investigation was to study the extent to which plant foliage was contaminated by fallout originating from nuclear detonations during Operation Teapot, 1955, and Operation Plumbob, 1957, at the Nevada Test Site.

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Materials and Methods

Samples of native plant foliage were collected from fallout contaminated areas within 250 miles downwind from the ground zero (point of deto-