

CATTAIL

THE SIGNIFICANCE OF ITS GROWTH, PHENOLOGY AND CARBOHYDRATE STORAGE TO ITS CONTROL AND MANAGEMENT



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ABSTRACT

A possible phenological and physiological basis for control has been suggested for use in cattail management work in Wisconsin. Cattail is a very important and natural part of most wetlands. It can provide desirable cover and nesting sites for waterfowl and other wildlife if it is properly interspersed with other plant species and open water. However, because of its ability to spread and dominate other plants, it can under favorable conditions completely close desirable semi-open habitat with solid cover.

Control and management methods to be most effective must take into consideration the strengths and weaknesses of the plant under Wisconsin conditions. The low period in carbohydrate reserves is the time when the plant should be most susceptible to injury and the period when control measures should be most effective. Phenological indicators can be used to determine the physiological low when carbohydrate reserves are minimum.

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STORAGE TO ITS CONTROL AND
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by

Arlyn F. Linde, Thomas Janisch and Dale Smith

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CONTENTS

- 2 INTRODUCTION
- 2 STUDY AREA
- 3 MATERIALS AND METHODS
- 3 Plant Development and Phenology
 - Sprouts and Aerial Shoots, 3
 - Rhizomes, 3
 - Seedlings, 3
 - Air Temperature, 3
 - Water Depth, 3
- 4 Carbohydrate Storage
 - Sampling Methods, 4
 - Preparation and Analysis, 4
- 4 RESULTS AND DISCUSSION
- 4 Plant Development and Phenology
 - Sprouts, 4
 - Leaves, 4
 - Factors Affecting Shoot Growth and Final Height, 6
 - Fruiting Heads, 9
 - Rhizomes, 13
 - Seedlings, 17
- 18 Carbohydrate Storage
 - Significance, 18
 - Relationship of Plant Parts, 19
 - Seasonal and Yearly Variations, 21
 - Relationship to Plant Phenology, 21
- 24 MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS
- 24 SUMMARY
- 25 LITERATURE CITED

INTRODUCTION

Cattails are not intruders into marshes but are very much a part of wetland ecosystems. They can provide a highly desirable type of habitat for marsh birds when they occur in proper interspersions with other marsh vegetation and open water. Because of their ability to proliferate and extend their areas of coverage, however, they may become the dominant plant community present, often to the detriment of the habitat and associated wildlife.

More precise control methods need to be developed that will break up solid stands of cattail and provide scattered areas of open water interspersed with cover of reduced density. Much of the work in the past that has been termed 'cattail control' has been done without special regard for the physiology and ecology of the plant (Linde 1969:123). Cattail control efforts in Wisconsin have

included plowing, discing, rototilling and herbicide spraying, usually at a time during the growing season when such work could be most conveniently fitted into the schedule. For the most part, these efforts yielded results ranging from moderately successful to poor.

Nelson and Dietz (1966) in Utah successfully conducted one of the few reported cattail control experiments that used a combination of mechanical and chemical control methods. They worked specifically during optimum periods for applying these controls.

Wisconsin studies indicate that Wisconsin cattail has different phenological and physiological adaptations than the Utah cattail, and that control methods must be modified accordingly (Linde 1971; Beule and Janisch 1973). A study was therefore conducted from 1971-73 in conjunction with the cattail management

and control experiments, specifically to document first the plant's development and factors affecting growth, and second, the cycle of carbohydrate storage and its relationship to phenology under Wisconsin growing conditions.

It is not our intention to offer specific control measures in this report, but rather to provide a better biological foundation on which to base existing and future management and control measures and to evaluate results. Status changes in carbohydrate reserves have already been worked out for many species of forage grasses (Smith 1969). This information is used to determine the potential of the plants to regrow following cutting or grazing. If cattail control and management measures are planned during the period when carbohydrate reserves are the lowest the chances for successful control of the plant should be greatest.

STUDY AREA

Our studies were conducted on the Horicon Marsh Wildlife Area (H.M.W.A.) located in Dodge County, Wisconsin (Fig. 1). The study area was confined to a small monotypic block of cattail in the southeast corner of the marsh. The cattail species present had many of the identifying characteristics of *Typha angustifolia*, including a definite separation of the pistillate and staminate portions of the spike, monadic pollen grains and narrow leaves. However, it also showed a considerable amount of variability suggesting hybridization. Although we did not pursue this matter, Smith (1968) in a vegetation survey on Horicon Marsh indicated he considered the hybrid *Typha glauca*, which is a cross between *Typha angustifolia* and *Typha latifolia*, to be strongly represented.

Horicon Marsh is a relatively shallow marsh with water depths outside of the channels and ditches not exceeding 3 ft. Water levels are regulated by a dam in the city of Horicon controlled by the Department of Natural Resources. An attempt is made to maintain more or less stable water levels but fluctuations often occur during periods of heavy precipitation and the high flow periods during the spring breakup. During the course of this study, water levels fluctuated widely. In 1971 they were near normal with an

average depth of 6 to 8 inches on the study area. However, during the spring and summer of 1972 the marsh was drawn down in conjunction with the Rock

River Chemical Treatment Program in an effort to eliminate carp from this segment of the Rock River. Water levels fluctuated widely on the study area from

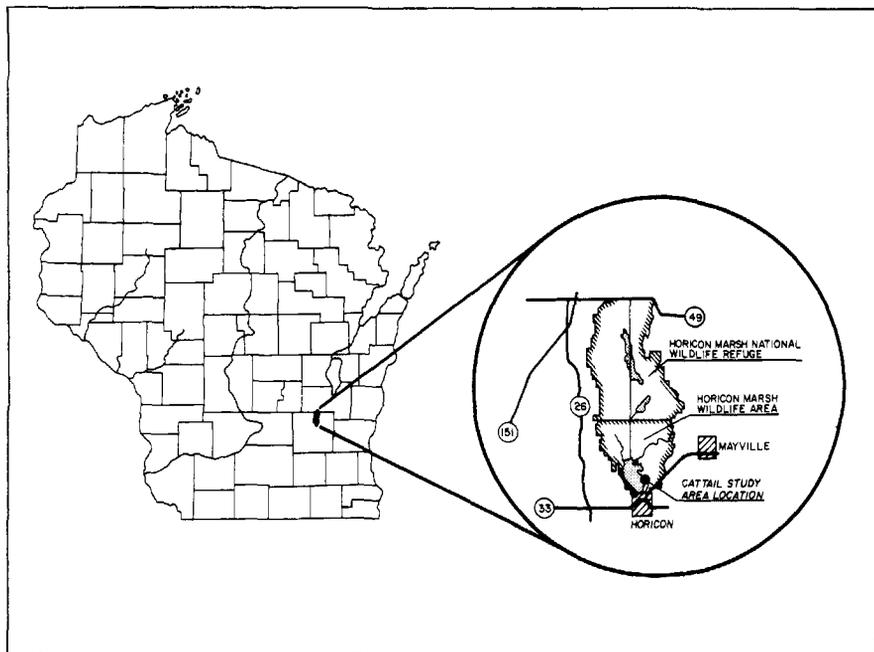


FIGURE 1. Location of cattail study area on Horicon Marsh Wildlife Area.

an almost total absence of surface water to near normal depths when heavy rains caused water levels to sharply increase despite the fact that the dam was open.

During the winter of 1972, three subimpoundments were constructed on the marsh. The cattail study plot was within one of these new impoundments. Because of impounding there was a drastic increase in water levels during the early spring of 1973. High water persisted until the middle of the summer when the dike was opened for placement of water control structures. Water levels on the study area then dropped and all surface water disappeared.

The East Branch of the Rock River

provides the main source of water for the H.M.W.A., or southern third of the marsh. The upper two-thirds of the marsh is the Horicon Marsh National Wildlife Refuge which is controlled by a dike and control structure located near the southern end of the refuge. Water for this portion of the marsh is received mostly from the West Branch of the Rock River; it is spilled into the southern third of the marsh, thus providing an additional source of water for the H.M.W.A.

Horicon Marsh is surrounded by uplands which are productive agricultural lands. Since the watershed is highly agricultural and the municipal disposal plants at Mayville and Waupun both

discharge their effluents into the Rock River, the waters coming into Horicon Marsh often carry a heavy nutrient load (Department of Natural Resources 1971). Water chemistry monitored at weekly intervals above the Horicon Dam during the years 1966-68, showed the following averages: pH — 7.8; total alkalinity — 282; and conductance — 645. Poff (1961) stated that carbonates (total alkalinity) averaged 195.2 ppm in the east central area of the state where Horicon is located. Our data therefore indicate that Horicon is in the high range within this hydrochemical region.

MATERIALS AND METHODS

PLANT DEVELOPMENT AND PHENOLOGY

Sprouts and Aerial Shoots

Cattail shoots used for measurement and study were selected randomly during 1971 and 1972. In 1973, in addition to 13 shoots originating from vegetative plants which had failed to fruit in 1972, 12 shoots were selected from 1972 plants which had borne fruiting heads. The number of study plants used each year was: 1971, 10; 1972, 20; and 1973, 25.

The number of plants studied was not large but we feel our data were representative since growth patterns between plants showed little variation. Although growth rates varied due to external conditions and individual differences, the manner which growth occurred and the order of leaf emergence and development was remarkably constant. All plants followed the same general pattern.

The reason for the increase in study plants in each succeeding year was to increase the opportunity for obtaining a representative sample of fruiting plants for study since there was no way of knowing in advance which plants would eventually fruit.

To provide a stable base for plant measurement, each study plant was provided with a graduated measuring stake in 1971. These stakes had a bottom cross piece located at the level of the plant base when the stake was inserted into place in the bottom soil. In 1972 and 1973 the wooden measuring stakes were replaced by 3-foot steel rods with angle iron cross pieces welded to them. Steel rods were

more slender than the wooden stakes and there was less likelihood of injuring the plants when they were inserted in the bottom soil. They were also more durable than the wooden stakes.

Initially, all measurements were made to the tip of the new sprout. As each new leaf began to separate from the leaf bundle it was given a number with a felt marking pen. Leaves were then measured individually at regular intervals. Measurements were made twice a week in 1971 and 1972 and once a week in 1973, and in all years continued throughout the growing season until leaf growth ceased.

Measurements were made to determine growth rate of the various portions of the fruiting head and also to record when maturity occurred. Careful notes were kept on the development and phenology of the plants.

Rhizomes

Five randomly selected plants were dug up weekly to observe new rhizome development. These observations began in April of 1972 and continued until August. During the first part of July in 1972, 13 rhizomes were randomly selected for studies involving growth rate and development. These rhizomes were measured in situ at weekly intervals until November 1972.

Seedlings

Cattail seedlings, which grew on one of the Eldorado Marsh cattail work areas in 1972, were measured for height at

weekly intervals throughout the month of July. Observations were terminated when the plants were destroyed during the course of other work on this area. Observations and measurements were also made on seedling plants which were produced on mudflats during the 1972 drawdown of Horicon Marsh. All work on seedlings was incidental to other work and no organized effort was made to specifically study these plants. However, enough observations were made to provide useful information.

Air Temperature

Air temperatures used in this study were the daily mean air temperatures as recorded by the U.S. weather station at Horicon, located 3 miles south of the study area.

Water Depth

In 1971 and 1972 water depths were measured at measuring stakes each time growth measurements were made. Measurements were also made in 1973, but toward the end of the growing season water depth was measured only at locations where study plants were actively growing. It was possible to relate 1971 and 1972 depth measurement readings to the Horicon Dam gauge readings. This provided a common base for interpreting measurements between these two years. In 1973 water levels on the study area were independent of dam levels because the study area became part of a new

subimpoundment. A staff gauge was installed in the subimpoundment and leveled in terms of the Horicon Dam base datum. This allowed us to make the necessary interpolations between years.

CARBOHYDRATE STORAGE

Sampling Methods

To supply material for carbohydrate studies in 1971, an old rhizome (one produced during a previous year) and a new rhizome (one produced during the 1971 growing season) were collected from each of 5 and sometimes 6 plants randomly selected on the study area. Collections of this type were made weekly beginning June 21 and continuing into the third week of September, well after

all leaf growth had ceased on the study plants.

A single additional sampling was made from four plants for total nonstructural carbohydrates (TNC) and then fractionated further into sugars and starch to determine variations in carbohydrate storage in various portions of the lower 8 inches of the aerial shoot and old and new rhizomes. TNC measurements are estimates of the carbohydrate energy readily available to the plant (Smith 1969).

Collections made in 1972 were made only from rhizomes which were actively producing aerial shoots. These were rhizomes which initiated development during the summer of 1971. A sample was taken from the proximal or older portion of the rhizome and another was taken from the distal or newer portion. This collection began April 16, 1972 and continued through June 29. It was not until the middle of June, when sampling was near its end, that new rhizomes

produced in 1972 were present in numbers sufficient for sampling. The 1972 new rhizomes were, therefore, not included in this sampling.

Preparation and Analysis

Rhizome samples were taken to the laboratory immediately after collection where they were thoroughly washed and then sliced into thin segments to facilitate drying. Each sample consisted of a rhizome length of approximately 5 cm. All material was dried between 66°C (151°F) and 70°C (158°F) for 92 hours and then packaged in plastic bags and stored until the summer's collection was completed. Materials were analyzed for TNC at the University of Wisconsin Department of Agronomy laboratory using a modified Weinmann method of removing TNC (Smith 1969).

RESULTS AND DISCUSSION

PLANT DEVELOPMENT AND PHENOLOGY

Sprouts

Sprouts began to form on the new rhizomes during the latter part of July and the first part of August (Fig. 2). The sprout, which is enclosed in sheathing leaves, constitutes a bud on the tip of the rhizome. The sprout contains in its base the meristematic region where leaf and flower primordia form and develop into the foliage and fruit during the next growing season. Once formed, most sprouts grew at a very slow rate the first year. Growth continued into November, or until freeze-up, at which time they became dormant.

Forty-three sprouts randomly selected in early November of 1972 had an average height of 7 inches (range 1 to 14 inches) before they went into dormancy. This figure for overwintering sprout height is probably somewhat biased since it is difficult to locate the shorter sprouts in the bottom muds.

Sprouts wintering over in a dormant state become active again the following spring as soon as air and water reach optimum temperatures for growth. In 1972, sprouts showed their first spring growth between April 27 and April 30. In

1973, only very minor growth occurred between March 29 and April 19, with the first significant growth coming after April 19. The growth rate in this year averaged 0.23 inches per day before the first leaf emerged. Some growth occurred even while ice was still present in the bottom substrate.

Leaves

All leaves begin their development from leaf primordia in the base of the sprout. As the sprout begins to elongate, the first leaf pushes out from between the sheathing leaves to begin development of the new aerial shoot. The leaves grow upward, differentiate tissues and mature. Growth is due to a proliferation of cells in the meristematic region and the elongation of these cells in the region just above it near the base of the growing leaf (Smith et al. 1936). We found that no growth occurred in the exposed leaf after it emerged from the leaf sheath, suggesting that this tissue is already in the maturation region. Growth in the base of the leaf pushes the maturing portions upward and new tissue behind it elongates and then matures to add to the leaf length from its base upward. Aerial shoots which do not develop fruiting heads are made up entirely of bundles of leaves growing from the subterranean

stem or rhizome. When fruiting shoots develop, they emerge from the center of a leaf bundle and are produced on a specialized branch or spadix.

The average date for emergence of the first leaf from the leaf bundle in 1972 was May 7. Leaves from shoots which later produced fruiting heads emerged an average of 4 days earlier than those of vegetative shoots. The second leaf usually appeared well before the first leaf reached maturity and ceased growth. It arose from within the center of the encompassing sheath of the first leaf with the flat or slightly concave surfaces of the leaves facing each other. Convex sides of both leaves face toward the outer edge of the leaf bundle (Fig. 3). As each succeeding leaf appeared, it emerged from the sheath of the leaf which preceded it. Leaves alternated their emergence from one side of the developing aerial shoot to the other (Fig. 3).

The number of leaves produced by a single aerial shoot in 1972 varied from 10 to 15. Vegetative shoots averaged 11.5 leaves while fruiting shoots averaged 14.2 leaves. The difference in number is accounted for by 2 spathe leaves which encompass the fruiting head. These are not true leaves but rather sheathing bracts for the fruiting spike (Smith et al. 1936). Unlike the true leaves which rise from the base of the shoot, the spathe leaves have their origin and point of attachment on the spadix, usually just

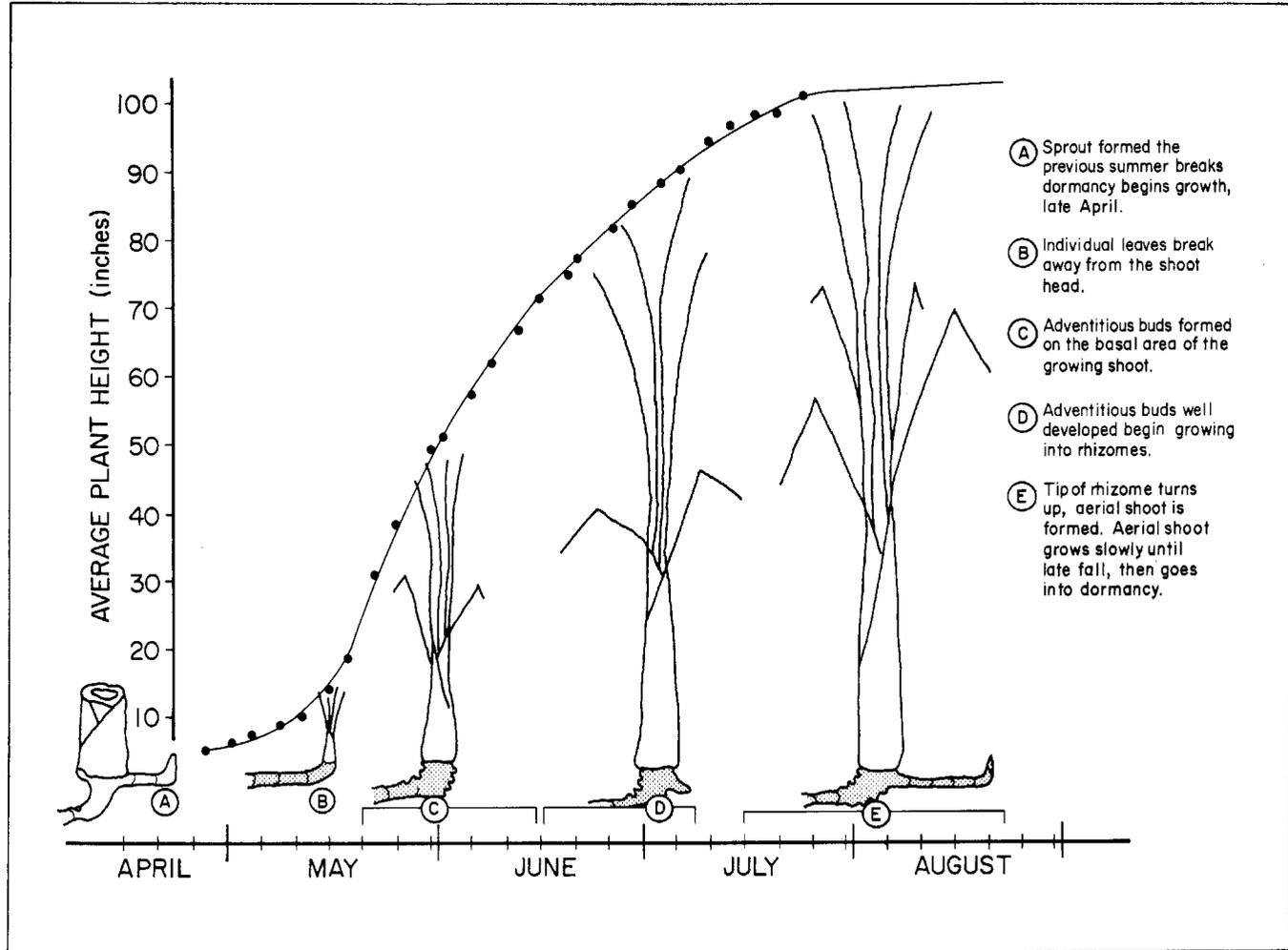


FIGURE 2. Phenology of development of below ground plant parts as related to the average plant height of the 10 vegetative study plants on H.M.W.A. in 1972.

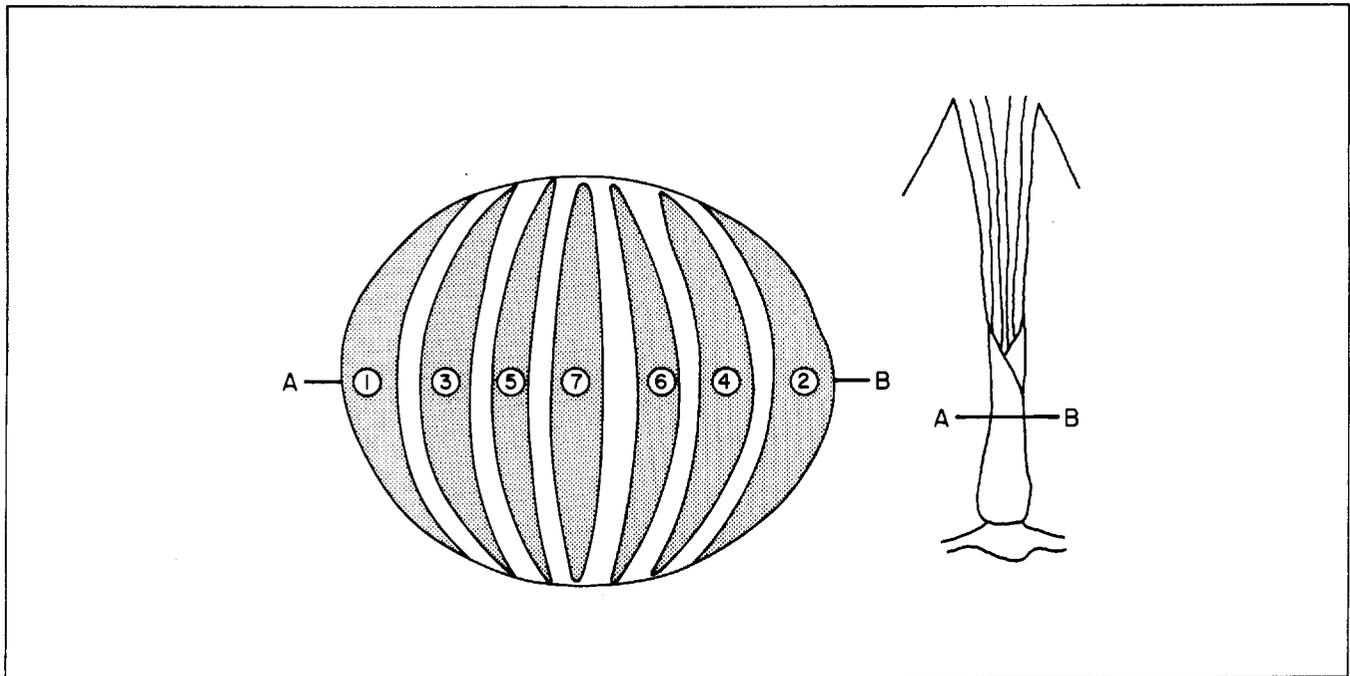


FIGURE 3. Schematic cross-section of cattail plant showing leaf form and order of leaf emergence from meristematic region.

TABLE 1. Comparison of final leaf heights in fruiting and vegetative plants, 1972.

		Avg. Height (Inches) at Termination of Growth	
Leaf		Fruiting Plants	Vegetative Plants
1		16.9	15.0
2		26.2	22.9
3		39.9	35.8
4		53.0	49.3
5		63.1	60.4
6		71.0	70.2
7		74.8	79.4
8		80.9	86.5
9		83.5	93.3
10		84.9	98.2
11		83.7	101.2
12		82.5	98.8
13		84.0	101.3
14		—	103.5
15		—	103.9
Pistillate Spathe		88.0	—
Staminate Spathe		81.6	—

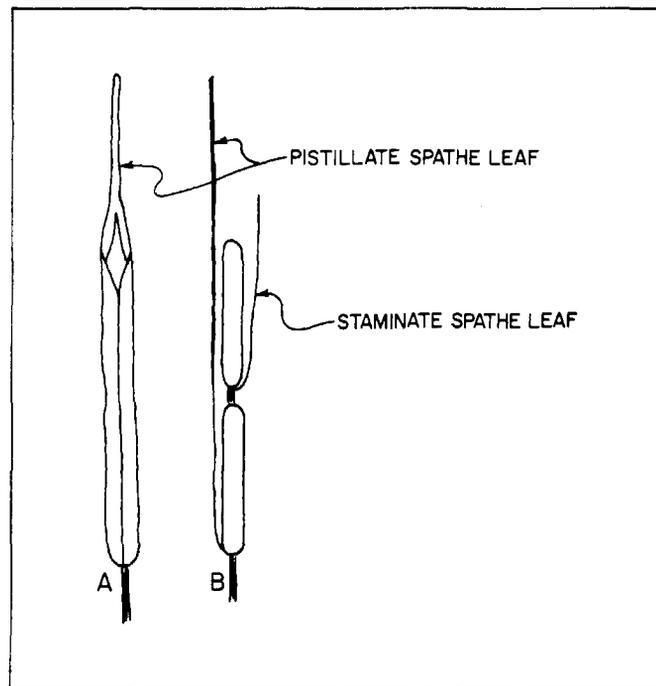


FIGURE 4. Fruiting head showing (A) envelopment by pistillate spathe leaf, and (B) points of attachment of pistillate and staminate spathe leaves.

below the spikes which they cover (Fig. 4). They are present for only a short period and fall off soon after the fruiting head emerges.

Nine of the 20 plants under observation in 1972 eventually fruited. The first 6 leaves to emerge on plants which later fruited attained a greater final height than the first 6 leaves of nonfruiting plants (Table 1). It is probable that the early quick growth of leaves of plants which later fruited may have occurred before the rudiments of fruiting head development began (Fig. 5). At this time the energy of the plant was concentrated into building as much photosynthetic surface as possible before energy was diverted to fruiting. After fruiting heads began to form, growth slowed down and the vegetative plants, which did not have this drain on their reserves, continued to produce leaf material for a longer time and grew taller. Meyer and Anderson (1939) noted that plants producing fruit tended to reduce their vegetative growth.

Each leaf increased the length of its period of active growth over the preceding leaf until a peak was reached. Periods of growth declined in length for the last 2 or 3 leaves. We found only 3 to 4 leaves actively growing on any one plant at a time.

Leaves of the vegetative plants grew for an average of 26 days following emergence from the leaf bundle, while leaves from plants which fruited grew only for an average of 17 days after they emerged. The last emerged leaf on fruiting plants completed growth an average of 30 days before the last emerged leaf on

vegetative plants. Leaf growth on fruiting plants ceased in late June as compared to late July or early August for the vegetative plants (Fig. 5).

Leaves on both vegetative and fruiting plants, as they matured and ceased growth, began to brown at the tip. This discoloration gradually extended downward as lower portions of the leaf, which were the last to finish growth, became senescent. Cattail stands containing many fruiting plants showed a conspicuous tan coloration to the foliage because of this early maturity and senescence.

Although each leaf on vegetative plants was usually longer than the one which preceded it, these differences in leaf length gradually became less later in the season. Usually, a leaf was produced later which had approximately the same length as the preceding leaf. After this, any further leaf production resulted in shorter leaves than the preceding leaves. All of the study plants that developed fruiting heads in 1972 showed this decrease in leaf height of the late produced leaves and seven out of ten vegetative plants also grew in this manner.

Since the vegetative shoots were composed only of leaves, the total plant height was the height of the tallest leaf at the time of measurement. Because each additional leaf was usually taller than the preceding one, the tallest leaf was continually changing and plant height through the season was a composite of all the tallest leaves present during the growing season. Total height in the fruiting

plants included the spathe leaves, when they were present. In some instances, the fruiting head itself added to the total height.

Factors Affecting Shoot Growth and Final Height

Average total height of the plants at the end of the growing season varied between years. There was a pronounced difference between plants which fruited and those which did not. Unfortunately, in addition to the expected variables in climatic conditions between years, there was also great yearly variability in water levels on the study area.

The rate of growth or amount of growth per day varied with environmental conditions and the stage of development of the plant as did total plant height. Of the factors we investigated, temperature seemed to have the greatest effect on growth rate, but water levels were of importance when depths became abnormal.

Effects of Temperature

Generally, high temperatures were associated with higher growth rates. However, other factors sometimes took precedence over temperature and the effects of temperature were then modified or masked. During the main part of the growing season in 1971 and 1972, temperature effects were usually quite

apparent (Fig. 6a,b). Plants nearing the end of their active growth period were noticeably less responsive to temperature changes than plants measured during the middle of their growing period.

As the leaves approached senescence little or no response to temperature was noted (Fig. 7). Growth rate and temperature were closely correlated for leaves in early stages of development, and there was low response to temperature for the same leaves as they approached senescence.

Growth is confined within a range of temperatures to which the plant is sensitive. This temperature range varies with the species. Raber (1933) stated that 41°F. is the minimum temperature for growth in most plants, 86°F. is optimum, and 113°F. is the maximum. Our data are based on average daily temperatures but periods of growth were within the temperature ranges described by Raber.

Water Level Fluctuations

The expected, or normal, water levels on the marsh usually involve uncontrolled high periods in the spring when precipitation and runoff are maximum. Highs also occur any time during the growing season when precipitation is heavy. The 'normal high' of 75.30 shown in Figure 8 is the level the management tries to maintain through manipulation of the dam. The 1971 water levels represented an approximation of normal yearly water levels. During that year, management was directed toward maintaining the 'normal high' water level.

In 1972 the dam gates were opened in March to accomplish a complete drawdown in conjunction with a carp eradication program. Because of heavy precipitation, the drawdown was slow during the first part of the summer and it was not until July that the marsh approached low

levels (Fig. 8). Complete drawdown was never achieved, however. Bottom soils were saturated and many pools of water remained. Although the dam gates were left open continuously through the remainder of 1972 and all of 1973, precipitation forced water levels up again in the fall of 1972. Normal high water was reached for a short period in the spring of 1973. Levels dropped with the advance of summer and associated high evapo-transpiration losses.

These drastic fluctuations in water level at the dam were reflected in the water levels of the study plot, but to a lesser degree. Since the study plot was well away from river channels or drainage ditches, drainage out of the bog mat was slow when water levels were low. Figure 6b shows the average water depth at 20 measuring points on various dates in 1972. Although the averages indicate that surface water was present through-

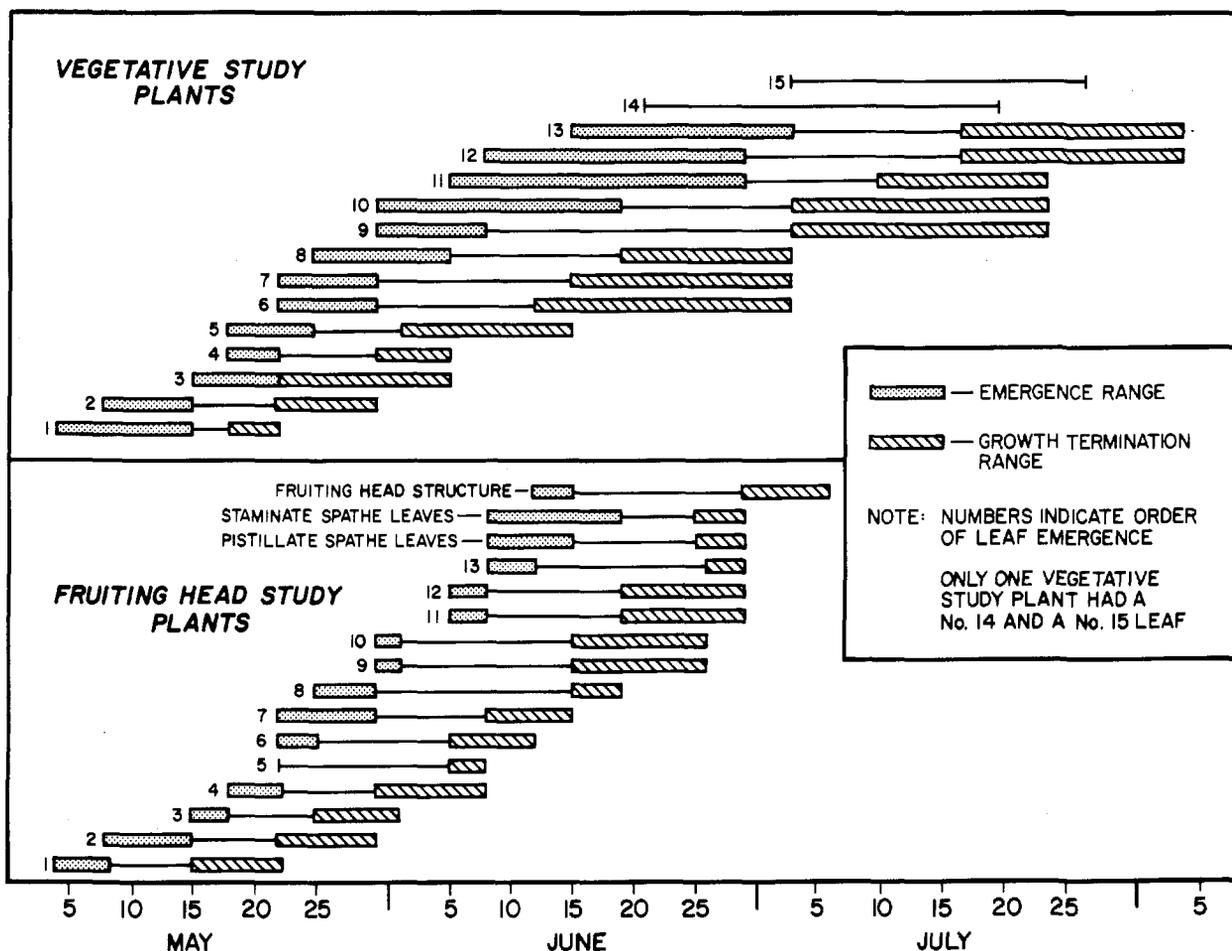


FIGURE 5. Average spans of emergence and growth termination for leaves of all study plants.

out the growing season, water actually did disappear briefly at some of the individual measuring locations, but the soil remained close to saturation at all times.

The extremely high water level in 1973 was brought about when diking for a new subimpoundment, which included our study area, was completed during the winter of 1972. Water became trapped behind the dike and water levels rose approximately 12 inches above the normal high water level for the study area. During the latter part of July a hole was cut in the dike to drain the impoundment and permit installing a control structure. At this time water levels dropped and the entire study area was drained of surface water by the first week in August.

In 1973 the extreme conditions which prevailed through the growing season certainly must have contributed strongly to the entirely different growth pattern which we found during that year (Fig. 6c). While growth rate in 1971 and 1972 paralleled temperature through the growing season until plant senescence began, this parallelism was not so evident in 1973. Temperature may have influenced the pattern from mid-May until mid-June but after that period any effect was over-ridden by other factors. About the middle of June, even though temperatures remained at a fairly high level, the growth rate dropped abruptly. Beginning the first of July and continuing into August, growth rates plateaued at a relatively low but constant rate. Leaf growth continued for nearly a month longer than it did in either 1971 or 1972.

Temperature variations between years do not account for this drastic change in growth pattern. The only environmental variable that was known to be markedly different was water depth. Indications are that rising water levels over a period of time tended to cause an increase in growth. In 1973 the growth rate increased throughout the period of gradually rising water levels (Fig. 6c). Shortly after water levels peaked and began to decline the growth rate went into an abrupt decline, then leveled off and maintained a constant slow rate of growth for almost two months. During this period surface water disappeared. This growth variation would seem to constitute an adjustment to the drastic alteration in water levels. Since water conditions were different each year of study, it is sometimes difficult to distinguish the effects of water depth from the effects of other variables in the environment. However, extreme variations in water level can be expected to occur on many wetland areas so this is another variable which must be considered when interpreting the progression of plant de-

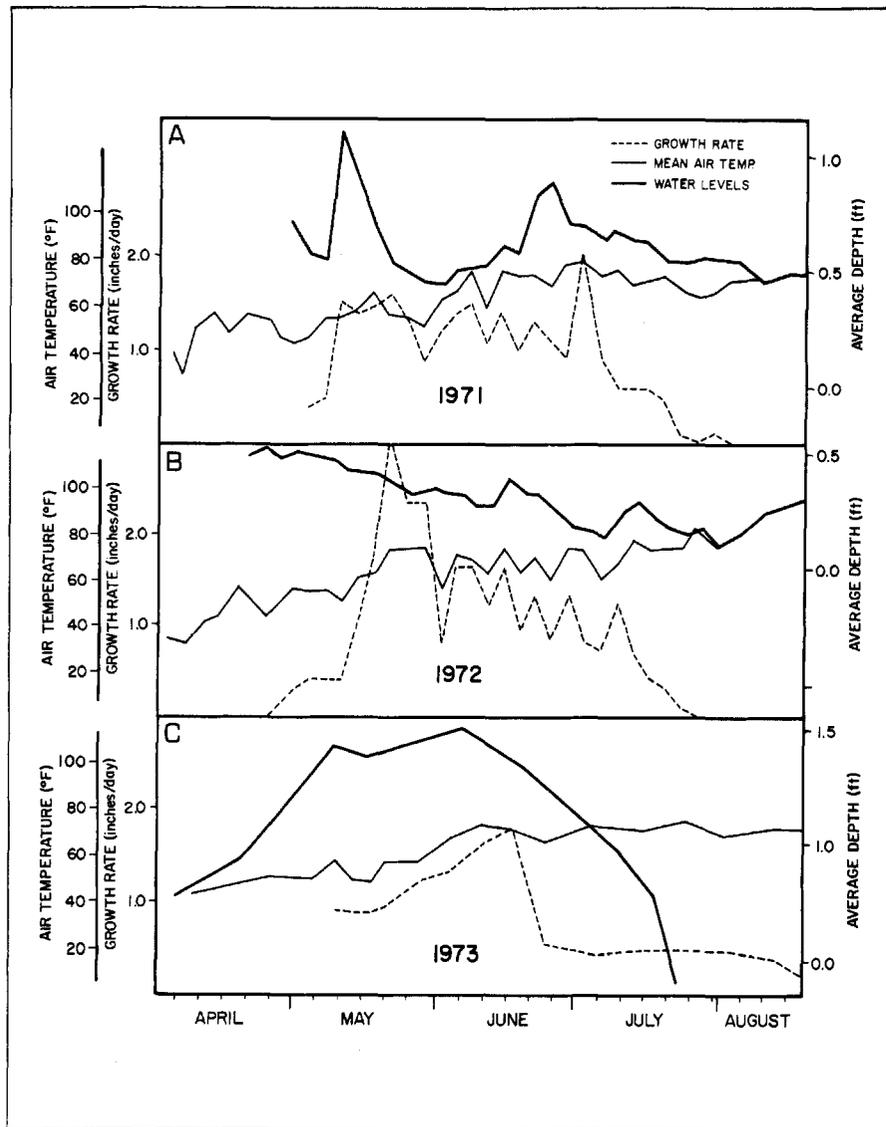


FIGURE 6. Relationship between plant growth rates, daily mean air temperatures, and water levels on H.M.W.A. over three growing seasons.

velopment and phenology for control purposes.

Fruit Production

Our data indicate that plants which fruited did not grow nearly as tall as vegetative plants produced in the same year. In 1972, the average final height of plants that fruited was approximately 15 inches less than the average final height of vegetative plants (Fig. 9). The seeming decrease in height at the crest of the growth curve for the fruiting plants is due to shedding of the spathe leaves at that point. Energy of the fruiting plants is apparently diverted from vegetative growth to the production of fruit. As a result, height growth in fruiting plants terminated early.

Fruit production may also be indirectly involved in determining the height of vegetative growths. Vegetative plant height varied from year to year on the study area with the 1971 plants showing greater height than the 1972 plants (Fig. 9). Relatively few fruiting heads were produced in 1971 and heavy production was experienced in 1972. Although we are discussing vegetative plant height rather than fruiting plant height, rhizomes interconnect in an extensive network and a single plant may cover a considerable area. Therefore, any particular vegetative shoot may be a part of a plant also producing other shoots which are fruiting. It is conceivable that the effects of reproduction may place a drain on all parts of the plant and result in smaller shoot height even in the vegetative shoots during a year of high fruiting head production. Meyer and Anderson

NOTE: LEAF NUMBERS INDICATE ORDER OF LEAF EMERGENCE

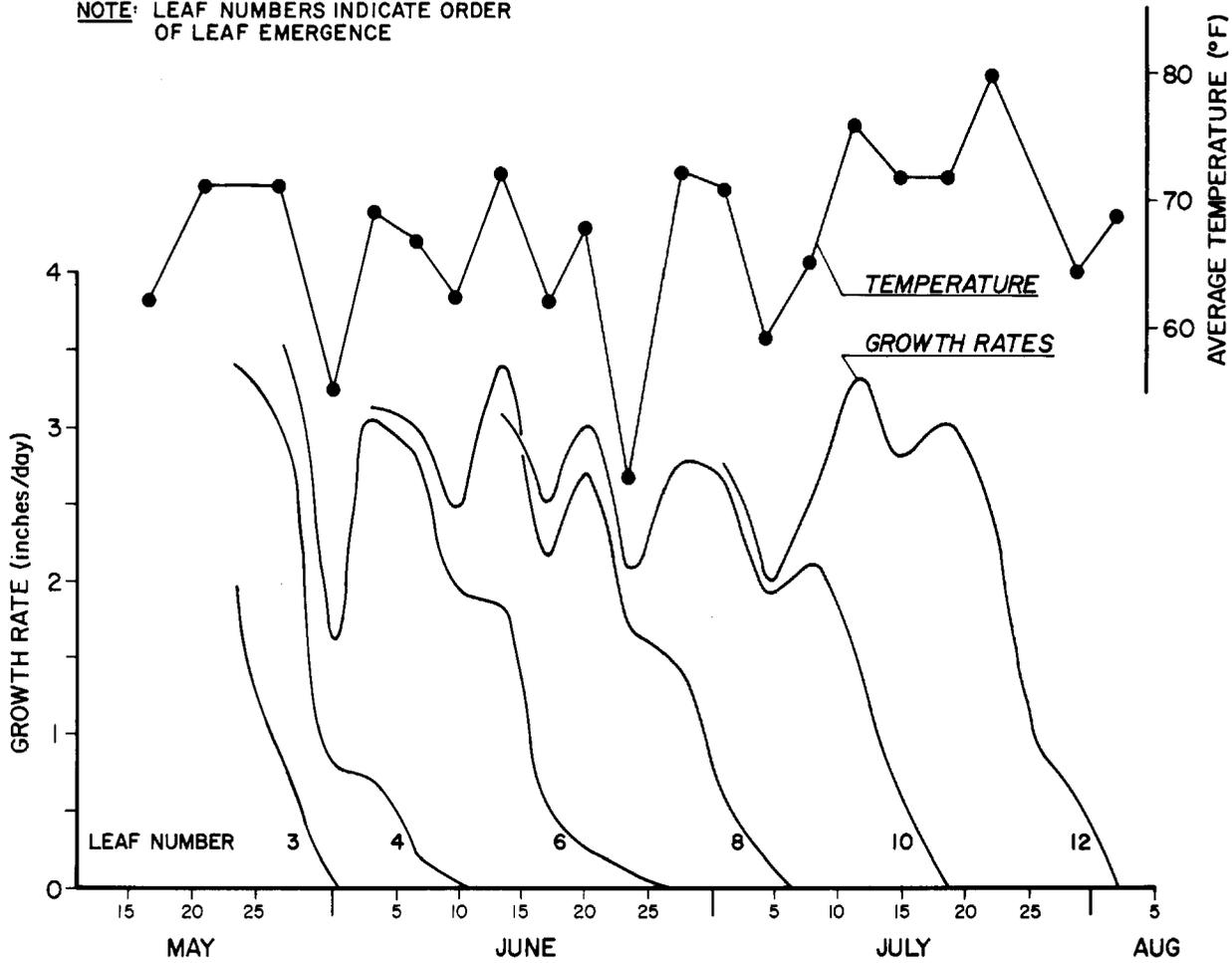


FIGURE 7. Growth rates of leaves on a vegetative study plant as related to mean air temperature.

(1939:618) in discussing the effect of reproduction on plant growth noted that the development of flowers often has a checking effect on vegetative growth. Conversely, if fewer fruiting heads are produced, the plants could use the extra energy for the production of taller leaves on all plants. Vegetative growth in 1973 was probably negatively influenced by the exceptionally high water levels rather than the previous year's fruit production. This is indicated by a somewhat distorted growth curve (Fig. 6c).

It is well known that some species of plants do not always bear fruit in quantity every year but rather alternate between a year of high production and year of low production. Raber (1933:279) stated that the crop of fruit the previous year may be a great drain upon the food reserves of the plant.

While Raber is not referring to cattail,

it is possible that heavy fruiting in cattail may also produce an imbalance within the plant which affects the next year's production of fruit. In 1971, although no actual counts were made, cattail fruiting heads were noticeably less numerous than they were in 1972 when a large crop of fruiting heads were observed. The ten plants selected at random for study in 1971 failed to develop any fruiting heads, while 9 out of the 20 plants observed in 1972 eventually fruited. In 1973, very few plants fruited on the study area and no fruit developed on any of the 26 plants under study. High water on the study area in 1973 undoubtedly influenced growth, but noticeably fewer fruiting plants were present outside the study impoundment also and here water levels were low.

The theory that cattail fruiting has an impact on growth and reproduction in the

following year was supported to some degree by the plants studied in 1973. Twelve of these plants originated as sprouts coming directly off from plants known to have fruited in 1972. Another 13 plants developed from sprouts on plants which failed to fruit in 1972. Separate growth curves were plotted for each of these two groups of plants (Fig. 10). Plants which originated from 1972 fruiting plants terminated growth at the end of the growing season about 5 inches shorter than the plants which developed from sprouts on 1972 vegetative plants. Also, when plants were dug up during the course of the 1972 rhizome studies, none of the plants which had fruit had originated as sprouts from plants which fruited in 1971. In other words, fruiting plants do not seem to vegetatively produce more fruiting plants the following year.

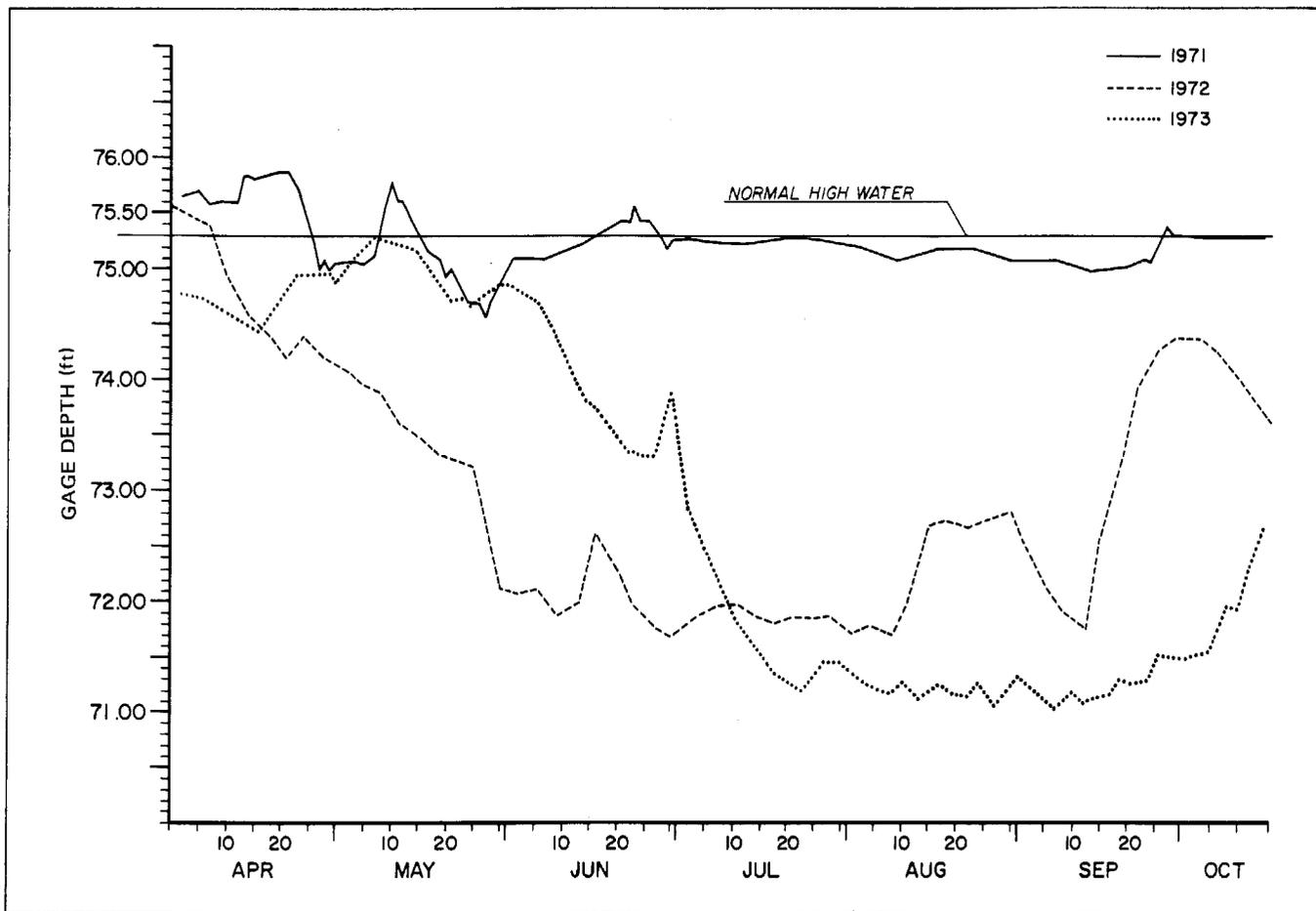


FIGURE 8. Horicon Marsh water levels at dam, 1971-73.

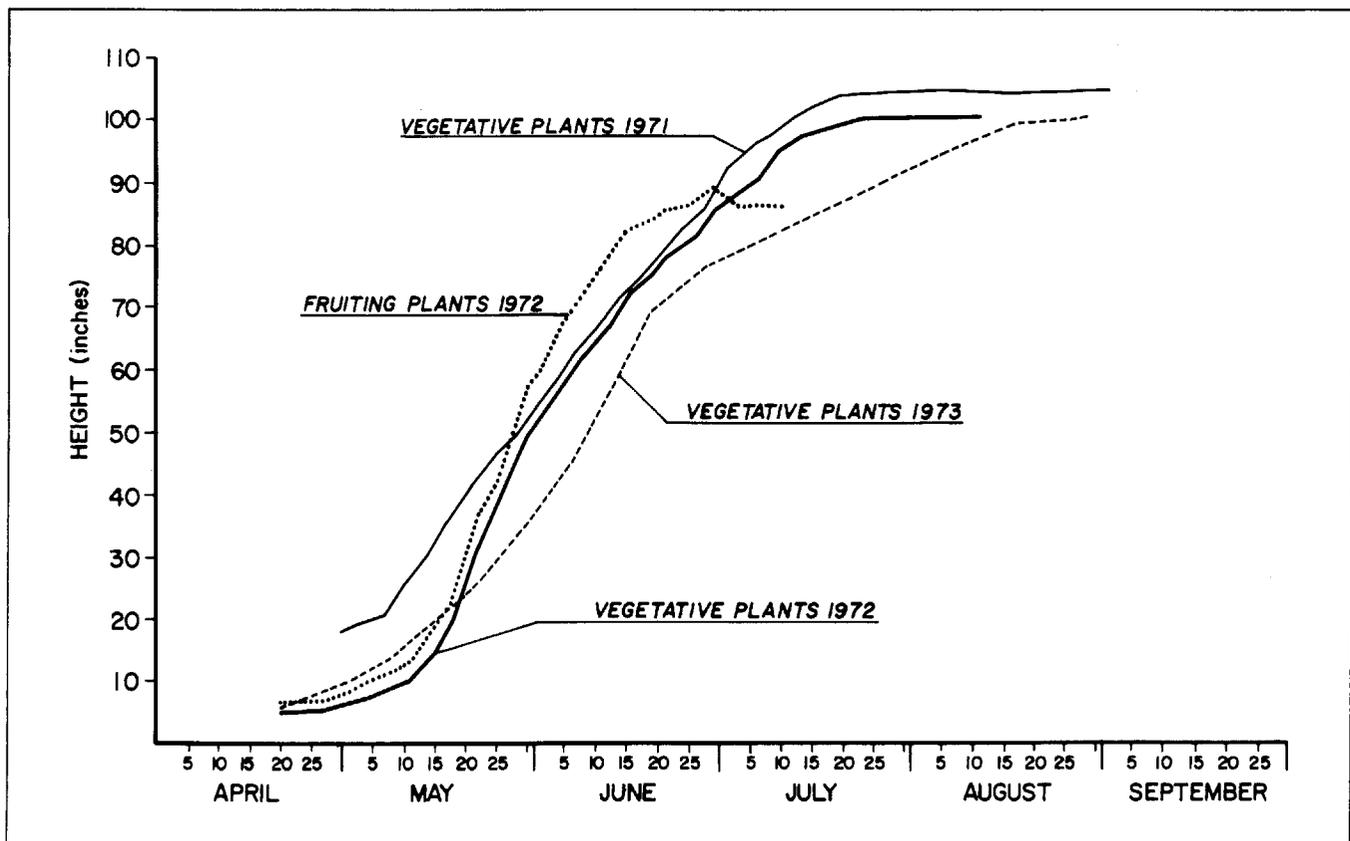


FIGURE 9. Plant growth in 1971, 1972, and 1973.

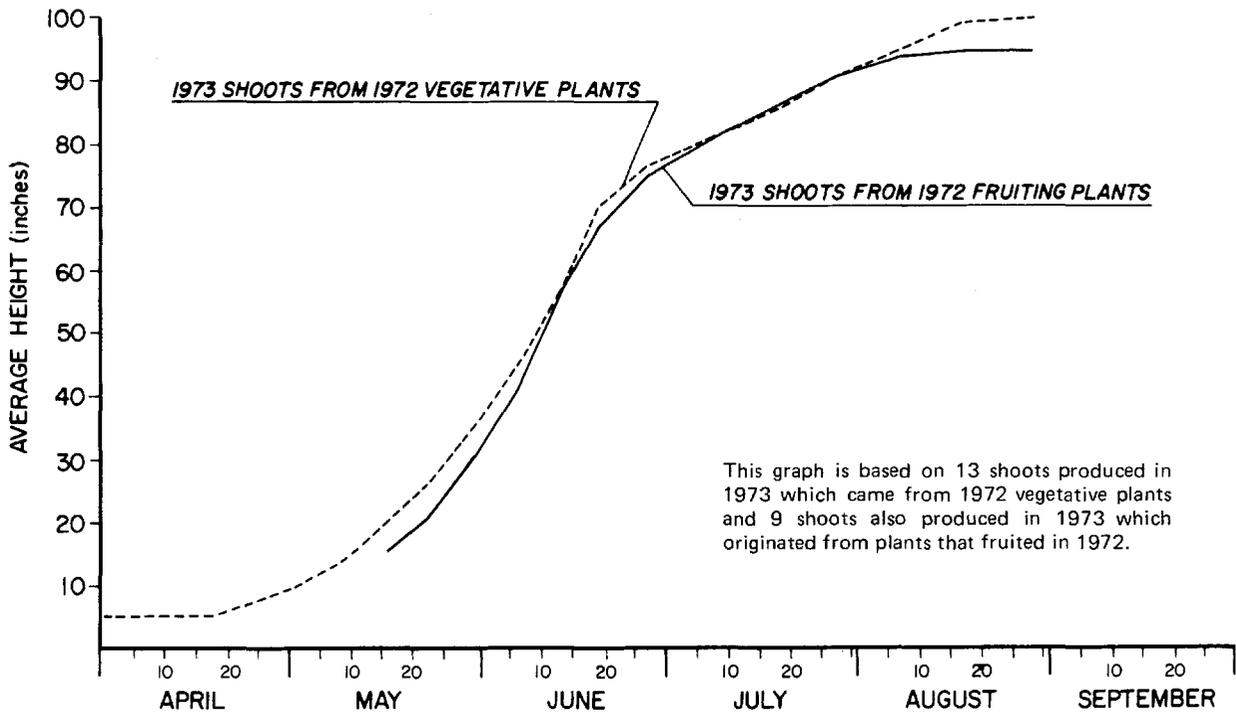


FIGURE 10. Growth of 1973 study plants.

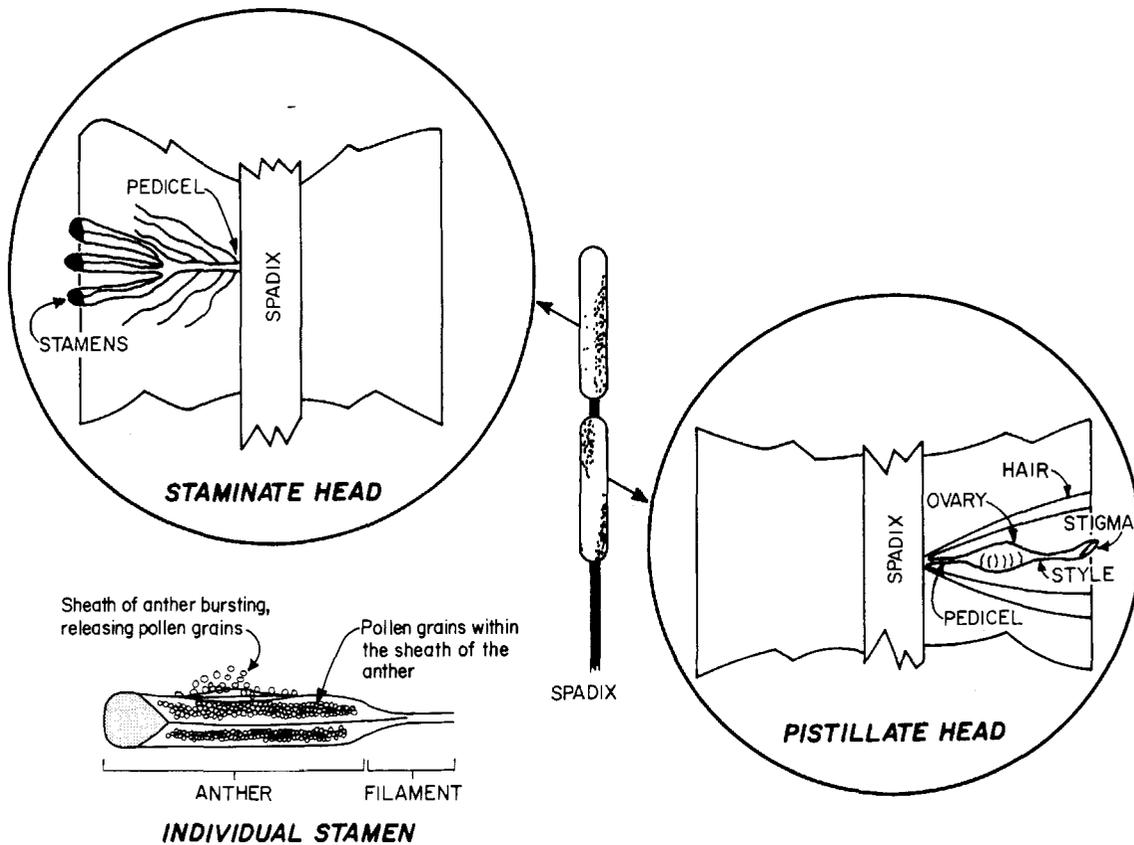


FIGURE 11. Cross-Section of the staminate and pistillate portions of a fruiting head showing details of flowers.

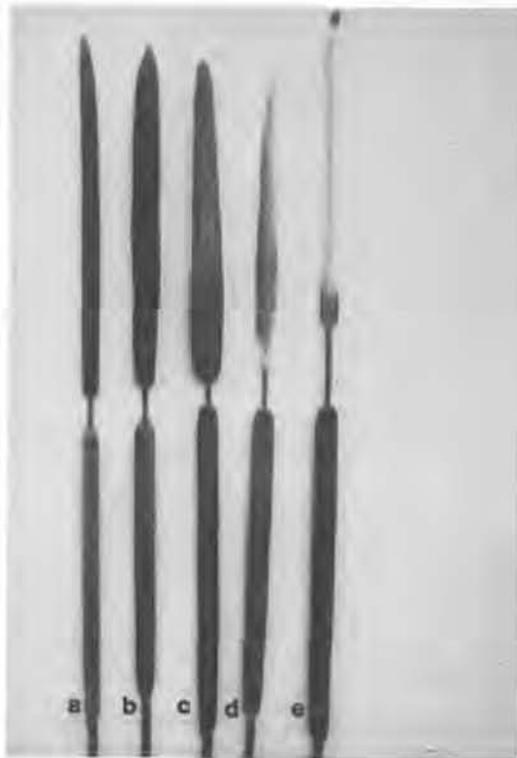


TABLE 2. Significant stages in fruiting plant development (9 Plants).

	Average Date	Range in Days
Maturity date of last leaf	June 27	10
Emergence of pistillate spathe leaf	June 11	7
Pistillate spathe leaf dropped	June 29	12
Emergence of staminate spathe leaf	June 14	11
Staminate spathe dropped	June 29	12
Avg. height of pistillate spathe at emergence	44 inches	
Avg. final height of fruiting head (To top staminate head)	84 inches	

This series of spikes shows various stages in the development of the upper or staminate spike and the relationship to the size changes of the lower or pistillate spike. Beginning from left to right: (a) Fully emerged staminate and pistillate spikes free of their spathe leaves. (b) Staminate spike beginning to expand in preparation for shedding pollen. (c) Pollen is shed beginning at the top and proceeding toward the bottom of the spike. (d) Pollen completely shed and all stamens in a state of atrophy. (e) Stamens have been mostly shed and much of the spadix which bore the staminate spike is now exposed.

Fruiting Heads

Spathe Leaves

The first visible evidence of fruiting head development was the appearance of the pistillate spathe leaf (Fig. 4). This leaf emerged from the center of the leaf bundle as a much narrower leaf than the normal vegetative leaves, and averaged about 27 inches long from its point of attachment. Unlike the vegetative leaves which had their bases located in the meristematic region at the base of the plant, this leaf was attached on the floral stalk at the base of the pistillate spike. It, therefore, moved upward as the flower stalk grew. Since this spathe leaf averaged about 12 inches taller than the top of the staminate portion of the fruiting head, it preceded the appearance of the fruiting head. Its sheath enveloped both the pistillate and staminate portions of the fruiting head and also enclosed the staminate spathe leaf which was attached to the floral stalk just below the staminate spike and extended approximately 7 inches above it. The staminate spathe leaf arose from the opposite side of the stalk from the pistillate spathe leaf and its sheath enclosed the staminate spike. At the time the spathe leaves first emerged from the leaf bundle no growth could be detected in the emerged portions of the leaf and all upward movement and further emergence was due to the elongation of the floral stalk or spadix. Increase

in height of the leaf exactly equaled the increase in height of the spadix to which it was attached, thus indicating that only the spadix was increasing in height. Apparently the fruiting head and its spathe leaves emerged fully elongated from the leaf bundle moving upward as the spadix increased in length. The spathe leaves were the last two leaves to develop in the fruiting plant.

Growth of the fruiting stalk after the head began to emerge was rapid. A maximum growth rate of 6 inches per day was recorded during the period from June 12 to June 15. Maximum leaf growth was recorded during this same period in fruiting plants at 7.3 inches per day.

The average date for emergence of the pistillate spathe leaf was June 11; staminate spathe leaves emerged an average of 3 days later. Average height of the pistillate spathe, when it first emerged, was 44 inches (Table 2). Unlike other leaves, the spathe leaves were retained by the plant for only a limited period of time. Average date for shedding both spathe leaves in the study plants was June 29. These leaves were much narrower than conventional leaves and they tapered sharply to the sheath.

Inflorescence

The cattail inflorescence is monocious, having both male and female portions in the same plant. The upper or staminate spike is the male component and produces

the pollen (Fig. 11). The pistillate spike is located below the staminate portion on the spadix and bears the female flowers which produce the seeds. In our study plants the separation between these two spikes averaged about 14 mm.

Staminate Spike. The staminate spike is made up of dense clusters of flowers, each consisting of 2 or 3 stamens borne on a short pedicel or stem. Around the base or each pedicel a number of hairs arise. The individual stamens have a columnar base or filament which is surmounted by a more or less spherical green head or anther giving it a match-like appearance. Pollen grains are produced in pollen sacs within the anther which, when development is complete, opens and liberates the pollen. At the time of pollination the pedicels elongate, pushing the stamens outward to give more space to the individual stamen for the release of pollen. The stamens are originally in tightly packed masses covering the spadix and produce a very dense spike with a pebbled green surface.

Measurements made on the diameter of the spikes during the course of their development indicated that the staminate spike built up to maximum diameter at the beginning of pollination and then dropped off in size as the pollen was shed (Fig. 12). Pollen began shedding at the top of the spike and continued down until the base of the spike was reached.

Plants began shedding their pollen between June 25 and June 29. As soon as the pollen was shed the stamens turned

- 1 BOTH HEADS 100% EMERGED FROM SHEATH BUNDLE
- 2 BOTH SPATHE LEAVES DROPPED OFF AND LAST EMERGED BASAL LEAF CESSATED GROWTH
- 3 PERIOD WITHIN WHICH POLLEN SHED
- 4 FRUITING HEAD STEM CESSATED GROWTH

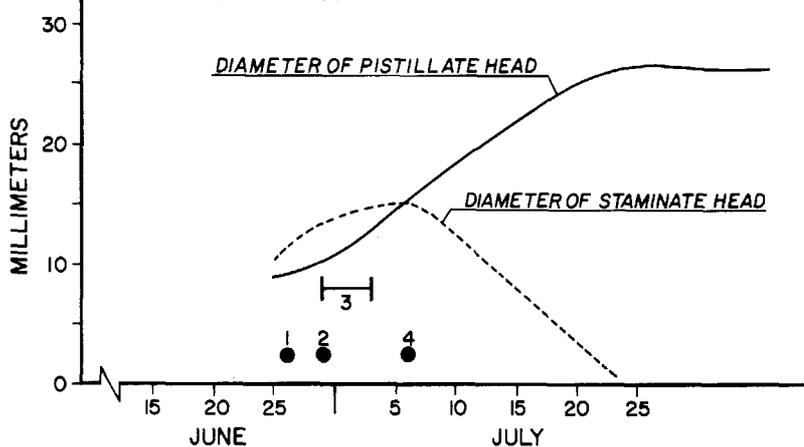


FIGURE 12. Phenology of fruiting head development for a typical study plant.

brown, wilted and began to shed from the spadix. By July 24 only the bare spadix remained. Eventually the spadix fragmented and broke off somewhat above the pistillate spike.

Pistillate Spike. The spike is covered with dense masses of flowers each bearing a single pistil composed of stigma, style and ovary. Each pistil, like the stamens, is connected to the spadix by a short pedicel (Fig. 11). Numerous hairs surround the base of the pedicel and these become the 'floss' which helps disperse the mature seed on the wind. Although no more than a single seed is produced in the ovary of each flower, flowers are so numerous that a huge number of seeds are produced on a single spike. Claassen (1921) estimated that an average *Typha latifolia* spike produced 250,000 seeds. Calculating the number of these seeds which were fertile and the germination rate, he concluded that a single spike was capable of producing 125,000 new plants. We made fruiting stem counts on a typical cattail monotype on the Eldorado Marsh Wildlife Area and found 4.4 fruiting spikes per square yard. If we apply Claassen's figures for seed production, there was a potential for producing more than a half million new seedlings from each square yard of cattail. While we acknowledge that Claassen's calculation may not be strictly applicable, since on Eldorado we are dealing with narrow leaf cattail (*Typha angustifolia*) which has hybridized, it does serve to emphasize the tremendous reproductive capacity of cat-

tail.

Morong (1888) estimated the number of fertile seeds in *Typha angustifolia* spikes to be between 60,000 and 100,000 seeds. This again indicates the enormous seed potential of the *Typha* genus. Whether 60,000 or 125,000 seeds are produced the potential for reproduction is still phenomenal.

Crocker (1938) found that *Typha* seeds could survive 5½ years of dry storage and still have a 70 percent germination. This high seed longevity coupled with its great seed production makes it quite apparent why cattail seeds seem to be omnipresent and merely waiting for the proper conditions for germination.

The pistillate head increased rapidly in diameter with pollination. Maximum diameter was reached in the study plants during the third week in July about the time the staminate head had completely atrophied. Seed development was occurring during this period.

Pistillate spikes had a mottled lime green color when they first emerged but this gradually changed to the traditional brown color as the stigmas and bracts became brown with maturity. Change in color occurred between June 29 and July 6 and the texture changed from a firm fleshy surface to smooth and mohair-like. By fall the brown stigmas began to break off exposing the white hairs which surrounded the seeds and the head took on a soft downy or whitish appearance. In late September, seeds began to shed as the

umbrella-like floss and attached seed broke loose from the spadix and was carried away by the wind. Many spikes do not break up in the fall and winter but remain more or less intact into the following spring. This serves to spread seed dispersal out over many months and probably has the effect of providing a better opportunity for at least part of the seeds to be shed during periods when conditions are most favorable for germination and development.

Rhizomes

Cattail plants are tied together by an underground network of stems or rhizomes growing parallel to the surface of the bottom. These stems interlace and interconnect and parts of a single plant may spread over a considerable area and have many aerial shoots (Fig. 13). This produces a colony or clone which reproduces vegetatively and migrates outward to invade new areas. All shoots are of identical genetic makeup (Curtis 1959) since they all originate vegetatively from a common ancestor. At Eldorado isolated clones of considerable size formed circular patterns which were clearly definable from the air (Fig. 14). Fassett (1957) stated that a clone which is an acre in size may consist of only a few plants. A single clone may put up thousands of aerial shoots which are composed entirely of leaves and occasional fruiting stalks. The true stems are confined entirely to the underground portions or rhizomes.

Rhizome Functions

The rhizome has a number of functions which are important to the survival and propagation of the cattail plant.

Carbohydrate Storage. The inner core of the rhizome is the principal area for storage of reserve carbohydrates (Claassen 1921). Reserves are built up during the growing season and stored through the winter to provide food during the period when the new aerial shoot develops in the spring and early summer.

Plant Extension and Migration. Growing rhizomes during the summer months move the plant beyond its periphery and cause it to 'migrate' into new areas. This is an effective means of vegetative propagation which continually puts the plant in suitable new habitat and maintains it where it is already established.

Winter Survival. The rhizome is an organ well adapted to carrying the plant through the winter dormant period. In addition to its central food storage core, it has a spongy cortex which contains parenchyma cells that are connected with the parenchyma cells of the aerial shoot (Claassen 1921). In the winter, even though the aerial shoot is dead these

Base of a mature cattail plant showing rhizome development and roots. Note that the rhizome tip is beginning to turn upward indicating that a new sprout will soon form and come to the surface.



Base of a plant which bore fruit showing new short rhizomes developing on the base of the parent plant. New rhizome growth on plants which have fruited is usually quite short.



Basal portion of a plant which has not fruited showing the new rhizome development and the up-turning sprouts. Plants which have not fruited usually produce longer rhizomes than the plants which have borne fruit.



arenchyma 'tubes' are capable of conducting air to the rhizome to which it is attached. Although rhizomes grow well under conditions of low oxygen and are capable of enduring anaerobic conditions for up to 13 days during dormancy (Laing 1941) they still need some oxygen to survive. Since most marshes become anaerobic for long periods during the winter months the cattail without this adaptation for securing oxygen from the surface would die.

Bud Formation

Rhizome buds began forming the third week in May on the basal portion of

the new growing shoot in our study plants. Four to six adventitious buds developed in a vertical line on either side of the basal area of the plant.

Rhizomes From Vegetative Shoots

Buds began elongating and became new rhizomes between the last week in June and the first week in July (Fig. 2). However, not all of the 8 to 12 adventitious rhizome buds developed into rhizomes. Most of them remained latent and only one or two developed into new rhizomes. Latent buds become active if the growing rhizomes or the aerial shoot

are injured or killed before they reach full development (Smith et al. 1936).

In order to determine if injury would stimulate rhizome bud development and bud proliferation in cattail, we initiated a simple experiment involving 4 growing cattail shoots having varying numbers of new rhizomes and buds. All of these plants were severely injured by removing the aerial shoot. In two instances we also removed part of the developing rhizomes. We found in all cases that injury seemed to stimulate the growth of existing rhizome buds and also brought about the proliferation of new buds, rhizomes and an aerial shoot (Table 3). On our study area it was uncommon to find 3 rhizomes

TABLE 3. Response of plants to injury, 1972.

Type of Injury, July 31	Buds Present Before Injury	Changes				
		August 4	August 11	August 22	September 1	September 12
Cut off all of developing aerial shoot (2 inches tall).	---	New bud formed below cut.	No bud growth; growth on cut shoot.	7/8 inch growth on cut shoot.	More growth on cut shoot.	No change
Cut off all of developing aerial shoot (7 7/8 inches tall).	---	1/4 inch long new rhizome formed below cut.	New rhizome 5/8 inches long.	New rhizome 3 3/8 inches long.	New rhizome 4 3/4 inches; tip turning up.	New rhizome 5 1/2 inches with 1 inch aerial shoot.
Cut off 3 rhizomes 12-14 inches long with developing aerial shoots.	1 bud	Bud development.	Bud 1/2 inch thick curving upward.	Rhizome nubs developing 7/8 & 1 1/2 inches long.	Rhizome nubs developed into aerial shoots 1 3/8 & 2 inches long.	New aerial shoots 2 1/8 & 2 1/2 inches tall.
Cut off 2 rhizomes and attached aerial shoots.	1 bud	Bud development.	Bud 5/8 inch thick curving upward.	Rhizome nubs developing 1/2 & 1 1/4 inches long.	Rhizome nubs developed into aerial shoots 1 3/8 & 1 5/8 inches long.	One shoot destroyed by muskrats; other shoot present and growing.

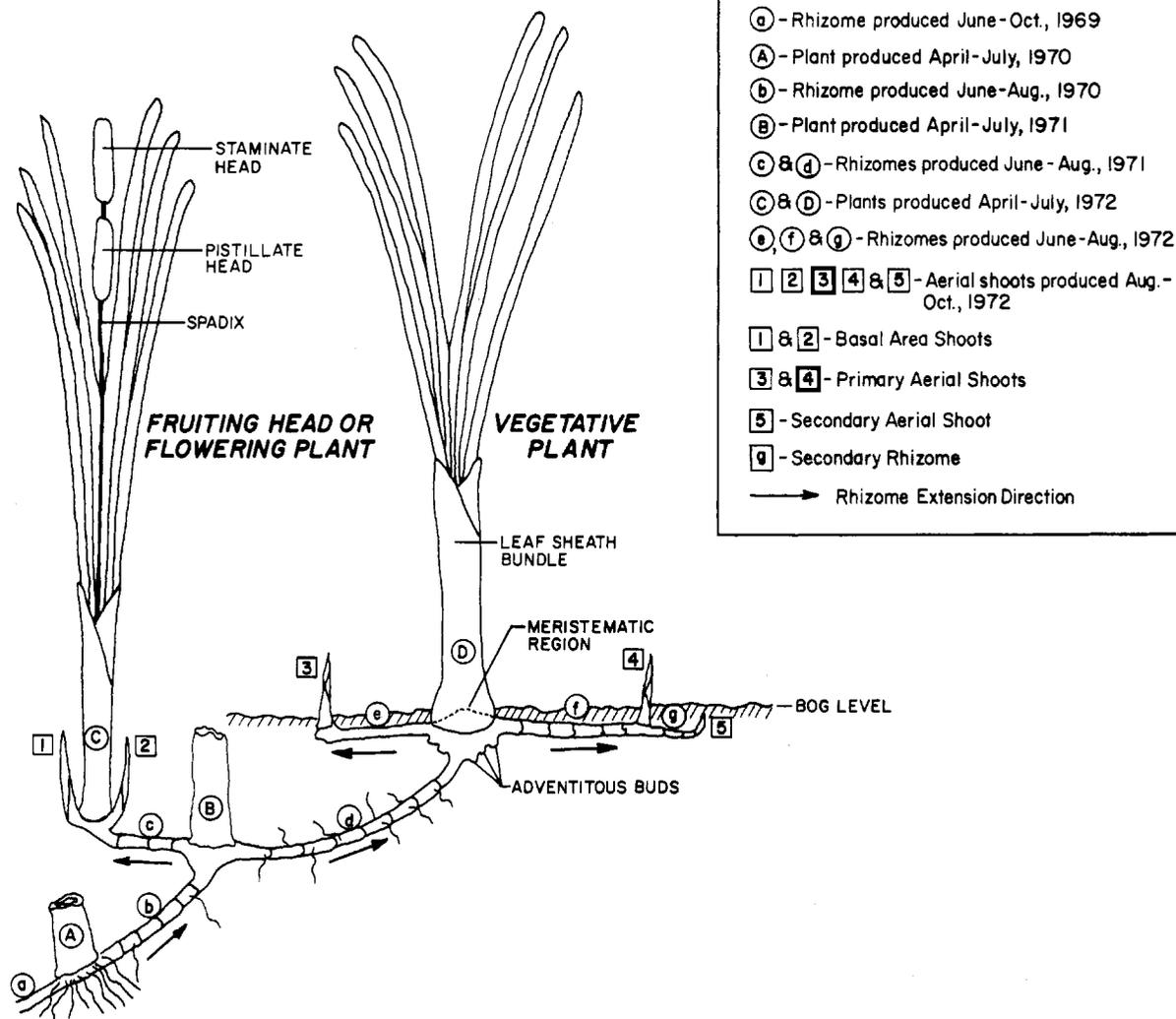


FIGURE 13. History of plant development and structures on 1972 study plants.



FIGURE 14. *Cattail colonies or clones form circular patterns which are tied together by a network of rhizomes. These clones may consist of only a few individual plants although the clone may be one or more acres in size. Note the circular clones in this aerial view of Eldorado Marsh.*



FIGURE 15. *Dense stands of new cattail plants developing during drawdown conditions on Horicon Marsh.*

developing from buds in the same basal area and rare to find 4. Rhizomes which developed from buds located in the basal area opposite the incoming old rhizome seemed to be most common and showed the greatest length. If 3 rhizomes developed, 2 of these were found growing opposite the incoming old rhizome. In the few instances where we found 4 actively growing new rhizomes, 2 of these grew from either side of the basal area of the mature shoot.

Rhizomes From Fruiting Shoots

Buds arising from the basal area of a shoot containing a fruiting stalk showed a different type of growth. Rhizomes were often absent and aerial sprouts developed directly from the rhizome bud with no horizontal growth or rhizome production (Fig. 13). Direct sprout development of this type was rare in rhizome buds developing from vegetative shoots. If rhizomes did develop on fruiting shoots they were considerably shorter than those found on vegetative shoots. The average length of fully formed rhizomes in vegetative plants was 10 inches with a range from 0.75 inches to 24 inches. Rhizomes produced at the base of fruiting plants, however, averaged only 1.9 inches with a range from 0 to 7 inches. The poor development of new rhizomes from plants which have fruited possibly is associated with a checking effect on vegetative growth caused by the developing inflorescence which requires that all available energy be diverted into its development (Meyer and Anderson 1939; and McNaughton 1966).

Secondary Rhizomes

In addition to the primary rhizomes which we have been discussing, secondary rhizomes occasionally occur (Fig. 13). These are produced from the base of a sprout on the tip of a new primary rhizome. We found this type of development occurring in 10 out of 60 rhizomes examined.

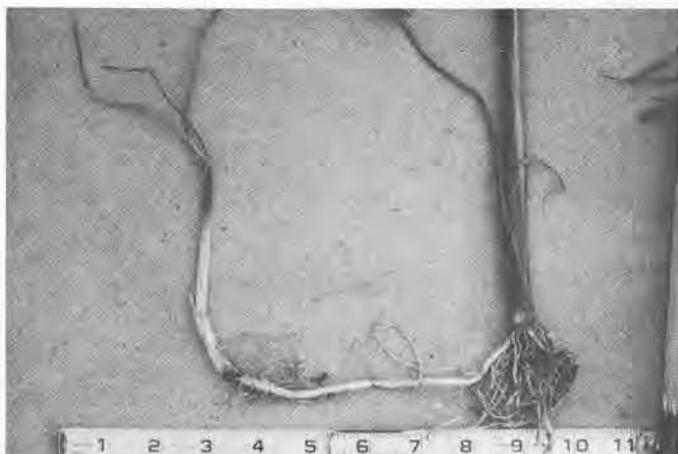
The average length of secondary rhizomes examined on our study area was 7 inches compared to 10 inches for primary rhizomes. The tips of the secondary rhizomes eventually turned upward and produced a secondary sprout. When both primary and secondary sprouts develop into aerial shoots the following spring, secondary rhizome production provides a means for increasing the number of aerial shoots.

Rhizome Growth

The meristematic region or growth area is located immediately behind the tip of the growing rhizome. Cells are proliferated here, elongate and eventually



Cattail seedlings of varying ages. These plants vary in height from 3 to 9 inches. Note the beginning of rhizome development in the larger plants.



This seedling cattail plant (on the right) produced a long horizontal rhizome which eventually resulted in the production of the new aerial shoot on the left.

mature pushing the growing tip ahead of them to bring about an elongation of the rhizome. Since a rhizome is actually a stem it develops nodes and internodes. The internodes rapidly elongate and mature, but the nodal regions remain embryonic and are capable of growth and differentiation after the internodal tissue matures. Three or four internodes may be proliferated before elongation of the cells begins (Smith et al. 1936). Elongation and maturation of each developing internode adds to the rhizome's length. Usually 9 or 10 nodes were present in our study plants before rhizome elongation ceased. Average length of the internodes was 1 inch and the maximum length was 3 inches.

New rhizomes, which had been growing parallel to the surface, changed direction during the third or fourth week in July and the tip began to grow upward and formed a new aerial sprout (Fig. 2). Further elongation of the rhizome then ceased. The meristematic region or growth area remains on the distal end of the mature rhizome, but leaf and flower primordia eventually differentiate from it and grow upward within the developing sprout.

The 13 measured new rhizomes on our study area showed an average daily growth rate in length of .36 inches per

day. Rhizome diameters ranged from 0.4 inches to 0.8 inches. The maximum growth rate recorded was 1 inch per day during the week of July 13 to the 17 in 1972. However, since rhizome measurements were not begun until rhizomes were already 3.9 inches long this growth rate may be subject to revision.

Seedlings

Seedling cattails grow and reproduce vegetatively in the same manner as shoots from established plants, but their size and rate of growth is much reduced. They appear to be miniature versions of established vegetative shoots.

Conditions Needed for Germination

Our observations indicate that maximum germination and production of seedling plants occurred on moist mudflats during severe water level declines such as occur during drawdowns (Fig. 15). When this decline occurred in the spring and very early summer the seedling plants had extensive development by

fall. Although moist mudflat conditions were ideal for cattail seed germination, shallow water of 6 inches or less may also produce new plants, but in lesser quantities (Bedish 1964; Bergman 1920; Wilson 1955).

Sifton (1959) found that cattail seeds are sensitive to white light and that germination is greatly reduced in darkness. He also noted that optimum temperature for germination is 30° C (86° F) and that below 25° C (77° F) germination rapidly falls off. However, wide alternations in temperature may stimulate germination even at low light levels. Germination is dependent on rupture of the seed coat which occurs in the presence of light and low oxygen pressure. These conditions cause the aleurone grains to swell and break the seed coat. Although germination is stimulated by low oxygen conditions, such as occur in saturated soils, respiration of the germinating seeds increases under aerobic conditions.

This may explain the greater survival of germinating seeds under mudflat conditions on Horicon Marsh. Saturated soils and accompanying low oxygen pressure promote germination. However, as the soil gradually loses its high water content and becomes aerobic, under mudflat conditions, respiration increases, thus increasing growth and seedling survival.

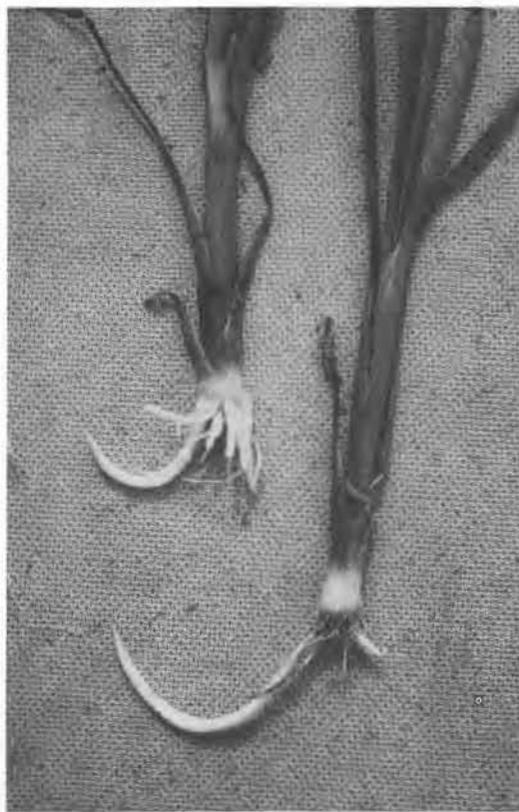


FIGURE 16. *Cattail seedlings which are developing substantial rhizomes.*

Leaf Growth

We observed four seedlings weekly for about 5 weeks during the summer of 1972. Development of the seedling aerial shoot proceeded in the same manner as it did when the shoot developed from rhizomes on existing plants except the shoot developed in miniature. One of the seedlings developed 6 leaves although it was only 3.4 inches tall (Table 4). In contrast, shoots originating from existing plants did not develop 6 leaves until they were approximately 40 inches tall.

During the period from June 30 to July 28 the seedlings had an average growth rate of 0.7 inches per day and the maximum growth rate was 1 inch per day (Table 4). This low growth rate and miniaturized development is probably to be expected since, unlike shoots from plants with a mature rhizome system that has a large reserve food supply for development, the seedling plant must produce all of its food through photosynthesis in its leaf surfaces.

Rhizomes

Rhizomes began developing on the seedling plants when the plants were still very small (Fig. 16). A seedling plant about 5.6 inches tall was found to have developed a rhizome bud and a 17-inch plant had two actively growing rhizomes. Another seedling about 23 inches tall had a 4-inch rhizome and from this rhizome a new shoot developed which was 10 inches tall.

Rhizome tips began turning upward in the soil to form new aerial shoots when the seedlings were 8 to 13 inches tall. When more than one rhizome developed they were located 180 degrees apart. Most of the seedling rhizomes were only about 3 to 4 mm in diameter at this stage so no appreciable amount of food storage was available. These plants therefore could be expected to be quite vulnerable to injury during the first summer of development.

TABLE 4. *Growth of cattail seedlings in 1972.*

Plant No.	Date	Height (Inches)	Growth Rate (inches per day)	Number of Leaves
1	June 30	3.4		6
1	July 7	6.5	0.4	7
2	June 30	5.3		6
2	July 7	8.9	0.5	7
2	July 14	13.5	0.7	8
2	July 21	19.0	0.8	8
2	July 28	21.5	0.4	7
3	June 30	9.8		5
3	July 7	14.5	0.7	8
3	July 14	19.9	0.8	7
3	July 21	25.5	0.8	9
3	July 28	29.3	0.5	
4	June 30	11.0		6
4	July 7	17.0	0.9	8
4	July 14	24.0	1.0	6
4	July 21	28.5	0.6	8
4	July 28	31.8	0.5	
Avg. Growth Rate			0.7	

CARBOHYDRATE STORAGE

Significance

Reserve food or energy is stored in plant tissues in the form of carbohydrates, such as sugars and starch. In perennials, such as cattail, these stored materials are primary sources of energy during the early period of growth in the spring when carbohydrates are utilized faster than they can be replenished by photosynthesis. An adequate reserve of carbohydrates at this time is essential if

the plant is to survive until photosynthesis can again supply its needs. To determine the reserve food present in cattail tissues, measurements were made for total non-structural carbohydrates (TNC). TNC measurements are estimates of the carbohydrate energy readily available to the plant (Smith 1969).

To effectively manage and control cattail, an understanding of its reserve food storage mechanism and the ability to estimate the time of low food reserves in relation to plant growth and phenology appears essential. During the period of low food reserves the plant should be vulnerable to injury by various control techniques. Periods of carbohydrate utilization and the resulting lows in reserve storage have already been worked out for many forage grasses (Smith 1972). This information is of great importance in determining when and how frequently a field may be mowed or grazed to obtain

maximum production without seriously injuring the plants. Since not all plant species have their low in food reserves at the same stage of growth (Smith 1972), it is essential that this low point be determined specifically for cattail so that there is an accurate base on which to develop management and control techniques.

Relationship to Plant Parts

Smith (1972) found that the carbohydrates most often stored in grasses are the monosaccharide glucose and fructose sugars, the disaccharide sucrose and maltose sugars, and the starch and fructosan polysaccharides.

He also pointed out that forage grasses can be divided into two groups based on the predominant nonstructural

polysaccharides accumulated in their vegetative parts. Grasses of tropical origin accumulate starch, while those of temperate origin accumulate fructosans.

Aerial Shoot

All forms of nonstructural carbohydrates were present in much lower quantities in the aerial shoot than in the rhizomes (Fig. 17). TNC increased progressively from the lower portions of the tightly rolled leaves down into the base of the plant, where starches were the most abundant fraction. In the leaves, most of the TNC was in the form of sugars. This indicates a continuing flow of materials from the leaves where they are manufactured, to the rhizomes where they are stored and later used in growth.

Meyer and Anderson (1939:570) noted that the cells of storage tissues are

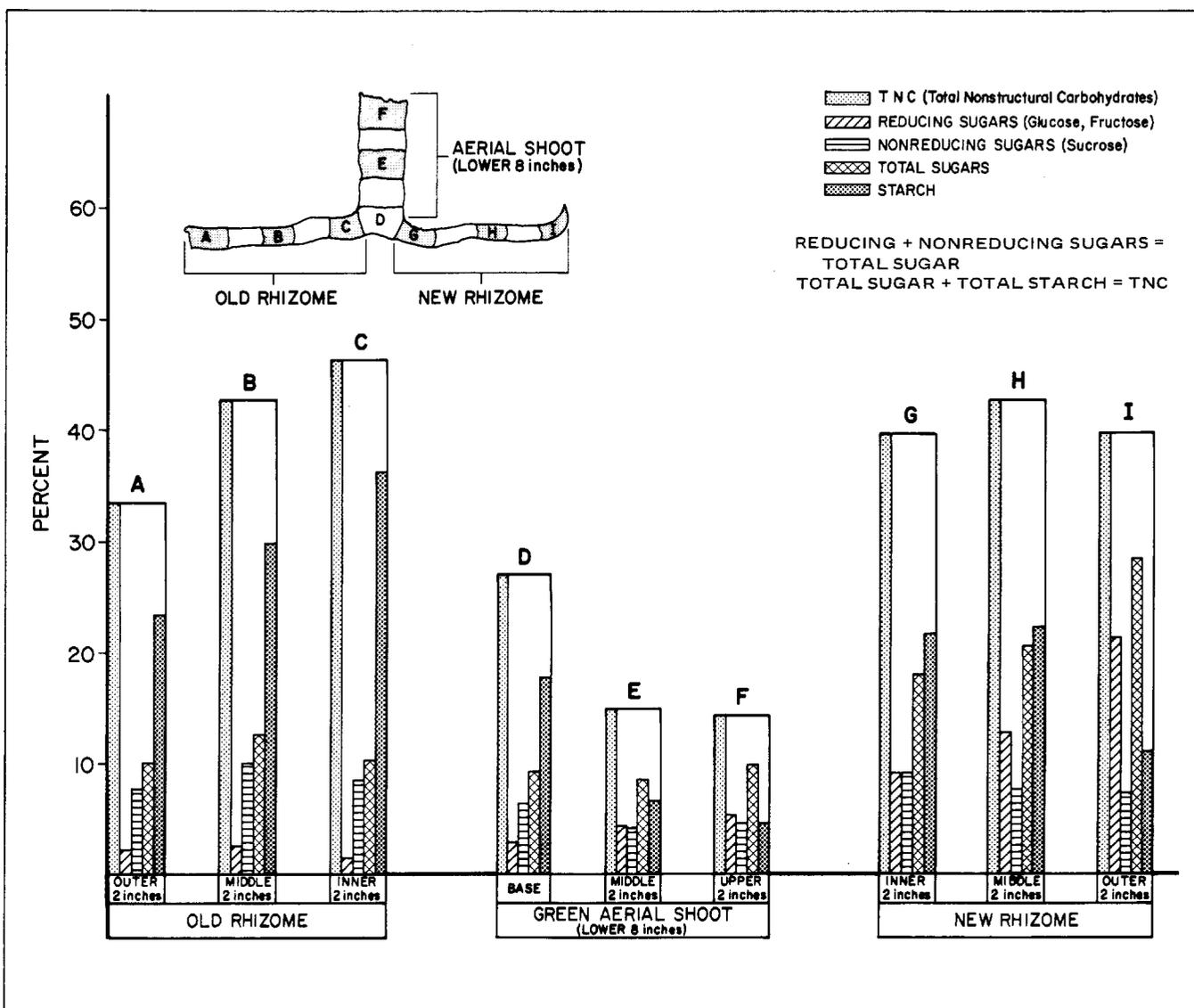


FIGURE 17. Carbohydrate concentrations in various plant parts (percent dry weight).

not merely passive reservoirs in which excess foods pile up. There is a continual change from soluble forms being translocated, to insoluble forms which are being stored, and back again into soluble form when they are used.

Old Rhizomes

Old rhizomes, those produced during previous growing seasons, seemed to be the principal storage organs (Fig. 17). Our data indicate that cattail is a starch accumulator, building up large quantities of starch in the old rhizomes. Sugars tend to be of much less importance. In August, when our samples were taken for sugar and starch analyses, reserves were accumulating rather than being used. Sugars present at this time were probably incoming materials which had not yet been converted to starch for final storage. The greatest concentration of TNC appeared to be in the proximal portion of the old rhizome where it was stored mostly in the form of starch. The amount of TNC decreased somewhat in the more distal portions. This may indicate that storage began in the proximal portions and gradually extended to the more distal portions with the passage of time. At the time of our sampling, TNC values were still recovering from the summer low, although by far the greater part of this recovery had already been accomplished. Since there was a higher TNC buildup in the base of the plant than in the lower parts of the aerial shoot, storage apparently began at this point and progressed out into the rhizomes.

New Rhizomes

Both old and new rhizomes contained approximately the same amounts of TNC, but the type of carbohydrates involved varied considerably between them (Fig. 17). In the new rhizomes (those produced during the current growing season) sugars became increasingly important, progressing from the proximal portion to the distal end or tip. Starches, which were in slightly greater amounts than sugars in the proximal portion, decreased in the tip to less than half the amount of total sugars present. In none of the other plant parts sampled were the reducing sugars (glucose and fructose) as plentiful as they were in the new rhizome — especially in its tip. Since these are the most soluble forms of sugar, it is probable that more of the incoming carbohydrates were being used in growth than were being stored as starches at this point. More storage occurred in the regions closer to the aerial shoot where growth was no longer occurring.

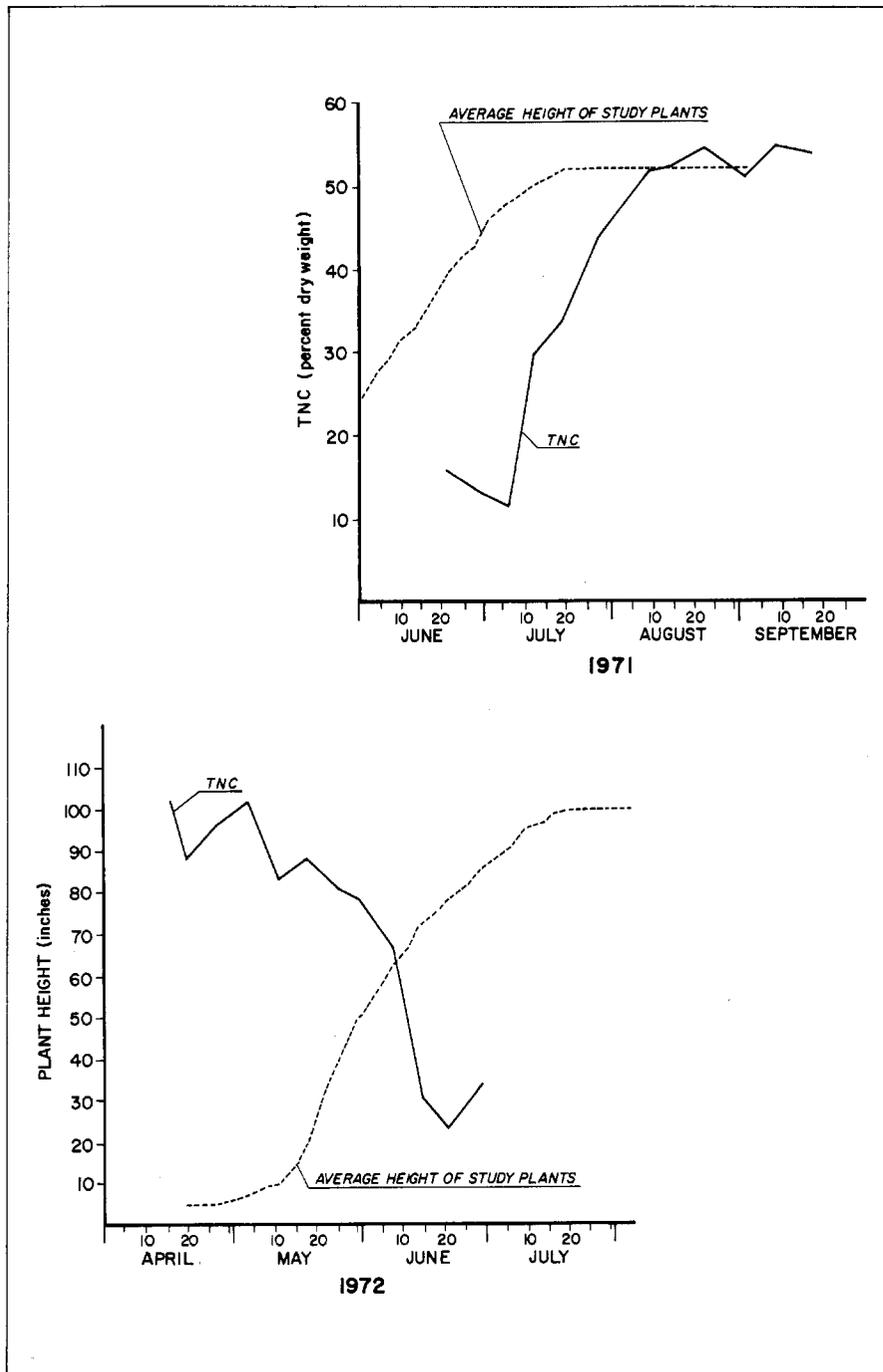


FIGURE 18. Seasonal changes in total nonstructural carbohydrates (TNC) in relation to plant height.

Seasonal and Yearly Variations

The seasonal buildup and use of TNC are shown in Figure 18. TNC reserves attained a low about 2 weeks earlier in 1972 than in 1971. One of the major differences between 1971 and 1972 was the large number of fruiting plants which developed in 1972. Our data indicated that a large production of fruiting plants may have caused a reduced total plant

height in 1972 as compared to 1971 because of the diversion of food materials into fruiting head production. Production of both leaves and fruiting heads may have increased the rate of reserve food utilization (Meyer and Anderson 1939) and these reserves were utilized sooner as a result. Plants in 1971 attained 91 percent (95 inches) of their average total height at the time the low in reserves occurred, while in 1972 they had attained only 78 percent (78 inches) of their average total height probably because of faster utilization of reserve TNC.

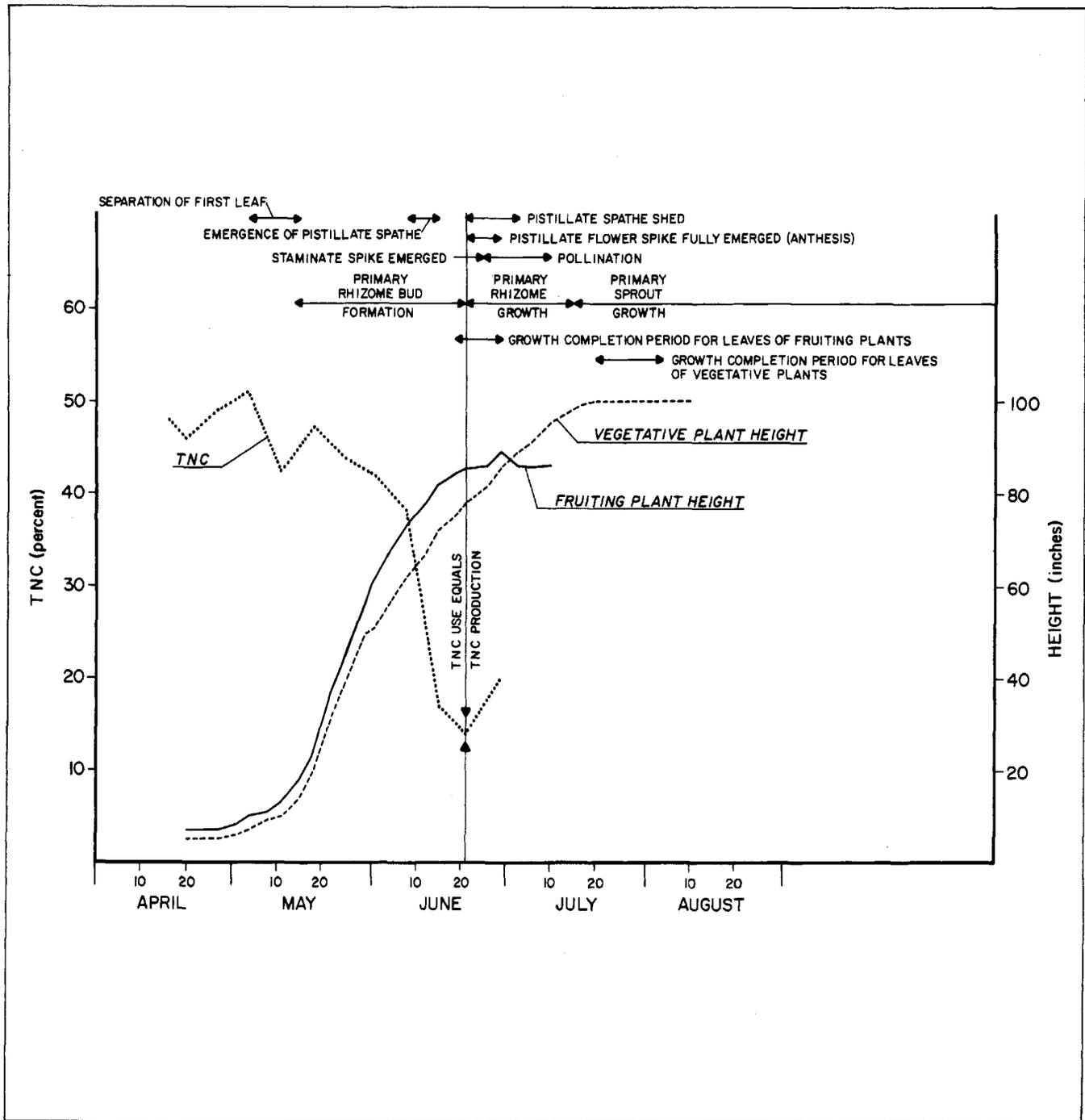


FIGURE 19. TNC reserves relative to plant phenology, 1972 (percent dry weight).

Relationship to Plant Phenology

TNC fluctuated in the early stages of growth during April and May when heavy drains on the reserves occurred during a relatively short period of time (Fig. 18). The minor rise in TNC following a drop probably represented a translocation of carbohydrates from one part of the plant to another in an attempt to compensate for the drain in TNC due to

growth.

The rate of carbohydrate translocation is not necessarily the same as the rate of its utilization. Replenishment of depleted tissues from stores in more remote areas could continue even though the growth rate had been severely curtailed. The first dip in TNC on April 20 (Fig. 18) was probably the result of first shoot growth in the spring. The buildup which followed may have resulted from a leveling out in the growth rate which allowed reserve food to be translocated into the depleted areas at a

rate faster than it was being utilized. During the period when the first leaf separated from the leaf bundle, intense growth again lowered the TNC reserves. However, plant height rapidly increased shortly thereafter and photosynthetic surfaces were being produced, which began to manufacture carbohydrates. This food production, coupled with translocated carbohydrate reserves, again permitted a slight recovery of TNC at the sampling point. However, as rhizome buds formed and fruiting heads began to develop, growth rate increased more

rapidly than carbohydrates could be manufactured and reserve food translocated. This resulted in a rapid decline in TNC at the sampling point until a low was reached on June 21. At this point TNC production equaled TNC use. This short period when plant reserves are minimum is the physiological low of the plant when it is most susceptible to injury (Smith 1972). Shortly thereafter, TNC began to increase as carbohydrate production exceeded food use. At this time fruiting plants had attained maximum foliage height and were heavily photosynthesizing.

We began sampling TNC during June in 1971 and continued until fall. In 1972 sampling was initiated in April when plant growth first began and continued until July to provide data which would coincide with those of the previous year. Although our data are not continuous between the two years, we have included the low in TNC for both years in the overlap area of the graph (Fig. 18). Note that although the low in TNC occurred during the same general period in the summer in both years, there is actually a two-week difference in the calendar

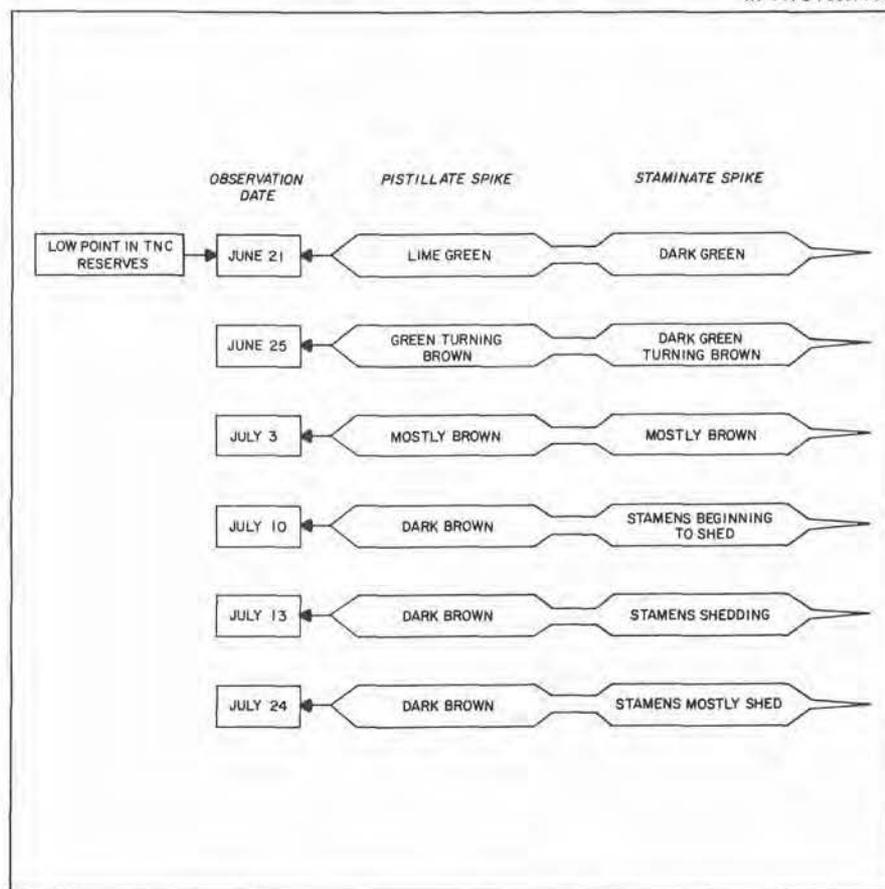
dates. This difference may be due to variations in environmental factors such as water levels and temperature which shifted the plants' phenology. It is obvious therefore that the low in TNC and the resulting physiological low of the plant are not fixed to a calendar date and will shift somewhat from year to year depending on external and internal factors.

A number of phenological check points were used to determine when this low in reserves occurred (Fig. 19). Calendar dates were useful only in a general way since variations among seasons, weather and other environmental factors caused variations in the plant's development and resulted in a shift in the plant's physiological low point. The best indicator proved to be the emergence and final shedding of the pistillate spathe leaf. This leaf emerged during the period when food reserves were suffering their fastest decline. At this time TNC dropped 14 percent in one week of time. Further reduction occurred and the physiological low was reached when the pistillate spathe leaves were beginning to shed and the plant came into full flower or anthesis. The exact date of the low point



Fully emerged floral head with both spathe leaves shed prior to the beginning of pollination. This point in the development of the floral parts should be close to the time when TNC reserves are at their lowest.

FIGURE 20. *Fruiting spike color changes relative to the low in TNC reserves.*



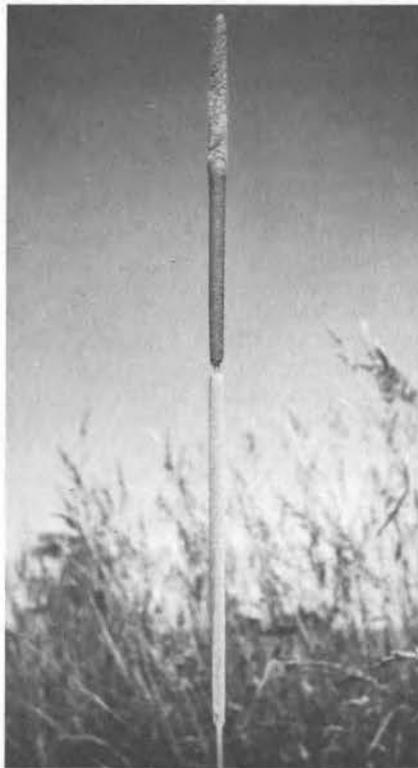
in TNC reserves occurred, therefore, at that time. These phenological indicators are easily determined for the period when the carbohydrate reserves have reached their low. At this point our study plants showed an average total height of 78 inches for the nonfruiting shoots and 86 inches for those that fruited. Leaves of the fruiting shoot had nearly reached maximum height at this time. Pollination occurred shortly thereafter.

At the critical point when carbohydrate reserves were at their lowest, the pistillate spike was lime green. The staminate spike was dark green (Fig. 20) and had a pebbled appearance. Shortly thereafter, TNC began to increase and the spikes took on a brownish tinge and lost their pure green color.

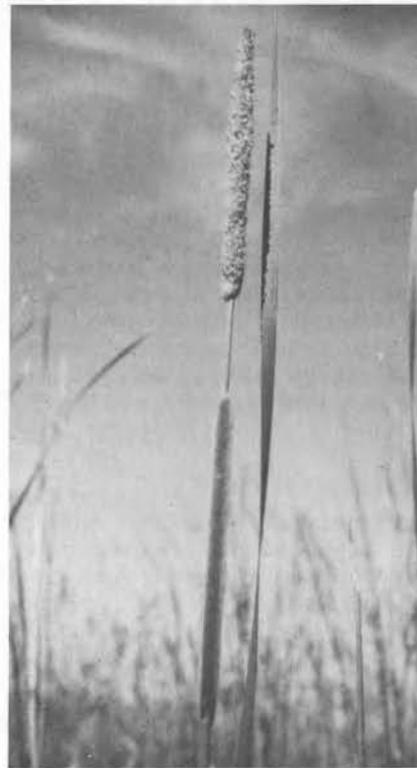
Rhizome buds, which had been forming on the base of the aerial shoot and its associated rhizomes, elongated into new rhizomes as soon as the TNC reserves began to recover from the low point. This elongation was completed just before the vegetative plants reached their maximum leaf height. At this time the rhizome tip turned up and the new sprout began to develop.



Cattail floral head with the upper or staminate spike just beginning to shed pollen. Note the staminate spathe leaf hanging down in front of the lower pistillate spike. This spathe leaf will soon be shed.



Fully emerged floral head with the upper or staminate spike in the process of shedding pollen. Pollination begins at the top of the spike and spreads downward until pollen has been shed from the entire spike.



Floral head with the upper staminate spike in the last stages of pollination. Stamens are beginning to atrophy.

Upper or staminate portion of the cattail head is beginning to atrophy. Note stamens at the top of the staminate spike have already been shed leaving the upper third of the spike bare and exposing the spadix.

Well-developed pistillate cattail spike. Note the bare spadix above this spike is bent over and broken. This is the portion of the spadix which formerly bore the stamens and staminate spike. These are now completely shed and the spadix is beginning to fragment at this point.

Fully mature pistillate cattail spike with seeds beginning to shed. Note the long white hairs which surround the seed and carry it on the wind are exposed and expanding.



Although cattail is persistent, spreads aggressively, and has a tremendous reproductive potential, it does have its weak points. Management measures planned on the basis of the weaknesses and strengths of the plant have a much better chance for success than those based merely on work convenience. Before attempting a management or control program, the following specific points should be considered:

1. For maximum control with a minimum of effort take advantage of the weaknesses of the plant in planning management and control measures. Although the low in carbohydrate reserves generally occurs in the latter part of June, utilize phenological indicators to help determine the exact time this low occurs since the calendar date will vary between seasons (Figs. 19 and 20). Since the low point in TNC is sharply defined and is easily missed because it occurs abruptly, TNC reserves are in a state of rapid change during the two-week period spanning the time just before and just after the low point. Our sampling was done on a weekly basis so the low could have occurred any time within the week indicated as being the low point. It might be well therefore to consider the week before and the week after the low point as a span when control measures will be most effective. This study involved hybrid cattail (*T. latifolia* × *T. angustifolia*) and narrow leaf cattail (*T. angustifolia*). Other species may show a different phenology.

Rhizomes need oxygen to survive over extended periods (Laing 1941), and this fact can be utilized in a management program if conditions are suitable for its application. Cattails, like other aquatic plants, have limitations on the maximum

depth of water they will tolerate. Water level can be used as a means of control and management if capabilities for raising and lowering it are flexible. However, deep water will do little good and much harm if the entire bog mat floats up when the water is applied. Although no attempt was made in this study to determine the maximum water depth, field observations indicated that narrow leaf cattail and its hybrid form seemed to thin out when water depths reached 2.5 feet. Harris and Marshall (1963) noted that *Typha latifolia* died out in water over 12 to 15 inches deep during three years of flooding and that hybrid cattail *T. latifolia* × *angustifolia* persisted in water depths up to 24 inches and the stands remained healthy.

2. Because they are produced in enormous quantities, cattail seeds are everywhere and merely waiting for the right conditions to germinate. Shallow water or mudflat conditions, while they produce many desirable food plants, are also conducive to the germination of cattail seeds. This should be considered when water levels are reduced for management purposes.

3. When planning management or control measures remember that cattail shoots are interconnected by a vast network of underground rhizomes and a single plant may cover many square feet of area. The plant not only spreads into new areas by these rhizomes but the rhizomes also serve as carbohydrate storage areas. When a shoot is severely injured it can draw on carbohydrate reserves in the rhizome network to produce a new shoot from latent buds which are commonly present.

4. Our data indicate that heavy fruiting puts an additional drain on the carbohydrate reserves. Therefore, control measures should be more effective during seasons when the production of fruiting heads is heavy.

5. Since it is obvious that not all shoots grow and develop at the same rate, average conditions will need to be approximated using as many of these phenological checks as possible on a reasonable sample of shoots.

Although we have pointed out the physiological weaknesses of the plant and have attempted to pinpoint these weak periods phenologically for management purposes, further research is still needed to develop improved control treatments based on these findings.

We have pointed out in this paper that the rate of growth and development in cattails varies due to such environmental conditions as water level extremes and temperature. The TNC reserves decrease during the spring and early summer growth period as growth rates increase and when fruiting head development occurs. It is obvious therefore that we cannot set in advance a calendar date when the low point in TNC reserves will occur and when the physiological low point of the plants will be reached. Since our data indicate that the low point in TNC occurs during fruiting head development we have attempted to develop a timetable which can be used to determine the physiological low period based on plant phenology. Phenological characteristics are annually recurring natural events in plant development whose calendar dates shift with environmental conditions.

SUMMARY

Cattail is a natural part of the wetland ecosystem and in a proper dispersion provides valuable nesting and escape cover for waterfowl and other marsh birds. However, it becomes a problem species when it rapidly proliferates and produces an unbroken monotype.

Much of the cattail control work attempted by game managers in Wisconsin in the past has been done whenever it could be best fitted into the work schedule rather than when it would

produce the best results. This usually resulted in mediocre or negative results. With this in mind, a two-part study was initiated by the Wetland Habitat Project in 1971. The objective of the first part was to study the phenology, physiology and carbohydrate metabolism of cattail under Wisconsin growing conditions. Findings from this work have helped to provide a firm biological foundation for the development of control techniques which have been investigated in the

second part of this study. Only the first part concerning biology of the plant is presented here.

The study was conducted on Horicon Marsh Wildlife Area during 1971-73. Cattail sprouts to be studied were located in the spring as soon as ice left the marsh. Development and growth of leaves, fruiting heads, and rhizomes were measured weekly throughout each growing season. Rhizomes were collected weekly to analyze total nonstructural carbohy-

drates (TNC). This was a means for determining stored energy levels on which the plant depends for initial growth and development in the spring.

Cattail leaf growth and total height paralleled mean air temperatures through June in 1971 and 1972. Gradually rising water levels during the 1973 growing season modified growth patterns noted during the first two summers of the study.

Adventitious buds at the base of growing aerial shoots developed into new rhizomes in early June. Maximum rhizome growth was 1 inch per day. Sprouts formed on the new rhizomes during late July and early August and these produced the next summer's crop of aerial shoots. These sprouts went into dormancy in late fall and resumed growth

usually in late April.

Leaves on plants which bore fruit ceased growth approximately one month earlier than leaves on vegetative plants and the final height of fruiting plants averaged 15 inches less than that of the vegetative plants. This indicated that plant reserves were probably being diverted from leaf production to fruit production and this resulted in a checking effect on leaf growth. Maximum leaf growth of the study plants was more than 7 inches per day.

TNC tests indicated that old rhizomes (those produced during a previous growing season) are the principal storage organs. The maximum level of TNC occurred during the early winter period. When growth was initiated in the spring TNC gradually declined to a minimum in

late June. Beyond this period carbohydrates were being produced in excess of the plant's immediate needs and they were translocated to the rhizomes for storage. Stored carbohydrates are available to help the plant recover from severe injuries and to develop new shoots the following spring before it is capable of photosynthesizing sufficient carbohydrates for its needs.

By correlating the low in TNC with phenological developments in the plant the critical period when the plant is most susceptible to injury was determined. The low in TNC in late June was found to coincide phenologically with the emergence and shedding of the pistillate spathe leaf. At this time, application of an appropriate control measure would probably achieve maximum control.

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INCHES	CENTIMETERS	FEET	CENTIMETERS	MILLIMETERS	INCHES
1	2.54	0.1	3.05	1	0.04
2	5.08	0.2	6.10	2	0.08
3	7.62	0.3	9.14	3	0.12
4	10.16	0.4	12.19	4	0.16
5	12.70	0.5	15.24	5	0.20
6	15.24	0.6	18.29	6	0.24
7	17.78	0.7	21.34	7	0.28
8	20.32	0.8	24.38	8	0.32
9	22.85	0.9	27.43	9	0.35
10	25.40	1.0	30.48	10	0.39
11	27.94				
12	30.48				
				20	0.79
				30	1.18
				40	1.58
20	50.80	FEET	METERS	50	1.97
30	76.20	1	0.31	60	2.36
40	101.60	2	0.61	70	2.76
50	127.00	3	0.91	80	3.15
60	152.40	4	1.22	90	3.54
70	177.80	5	1.52	100	3.94
80	203.20	6	1.83		
90	228.60	7	2.13		
100	254.00	8	2.44		
110	279.40	9	2.74		
120	304.80	10	3.05		
		20	6.10		
		30	9.14		
		40	12.19		
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		100	30.48		

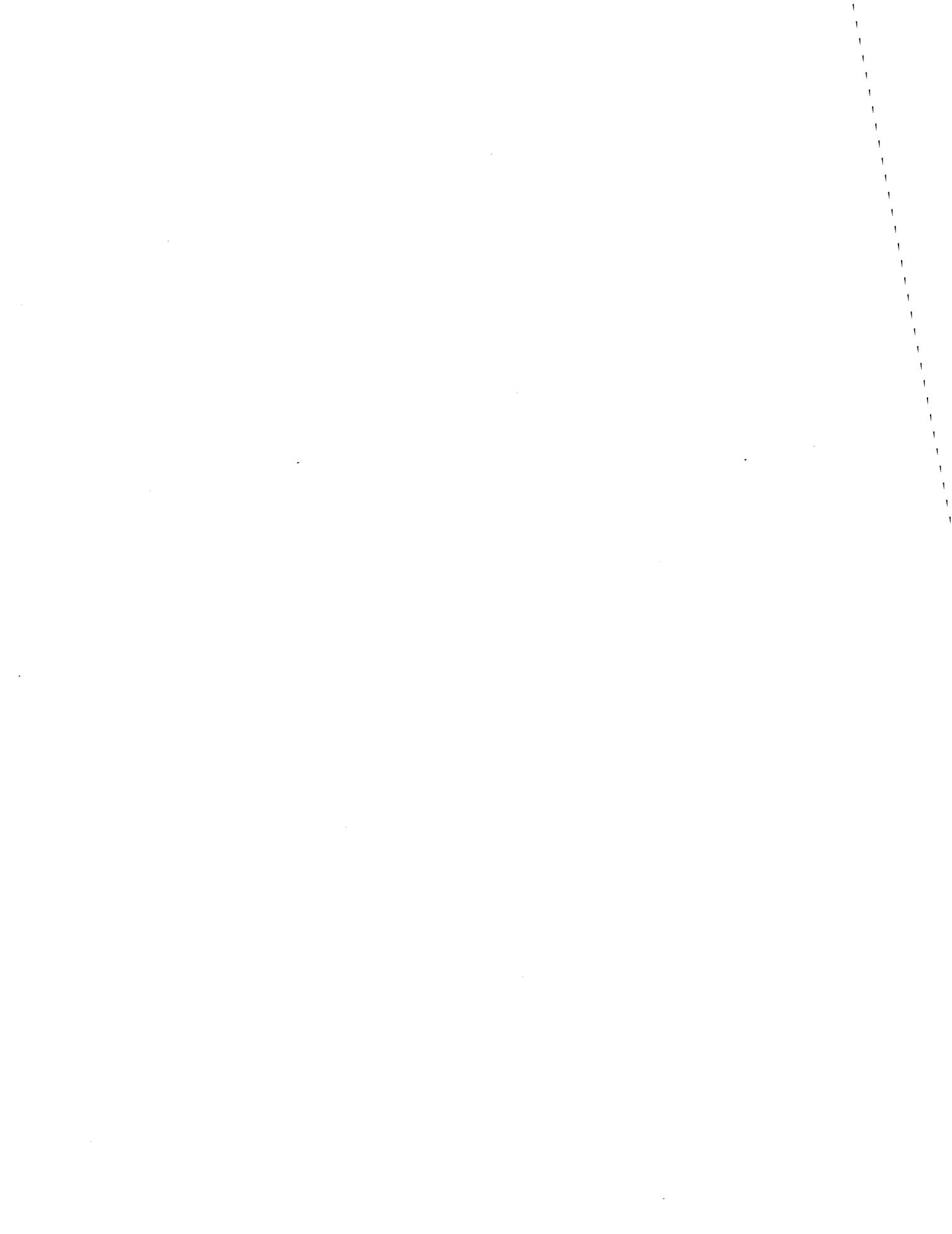
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About the Authors

Arlyn F. Linde is a Project Leader and Thomas Janisch a Project Assistant, in the Bureau of Research, DNR; Dale Smith is a Professor of Agronomy, University of Wisconsin-Madison.

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