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The impact of draining, burning and fertilizer treatments on the nutrient status of floating *Typha* mats in a freshwater marsh

Der Einfluss von Drainage, kontrolliertem Abbrennen und Düngung auf die Nährstoffverhältnisse in schwimmenden *Typha*-Beständen

Bertil O. Krüsi

1989

CONTENTS

1. INTRODUCTION

In cool, northern wetlands nutrients tend to be withdrawn from circulation through incorporation into organic matter and surface litter which accumulates because of slow decomposition in this type of climate (e.g. WEIN 1983). ROWE and SCOTTER (1973) called this process nutrient lock-up. WARD (1968) reported for wetland areas where water levels had been artificially stabilized that organic matter can accumulate to substantial depths in comparatively short periods of time that is 10 to 20 years. And WELLER (1975) found in a newly established cattail stand the formation of a 35 to 43 cm thick mat in as little as 3 years. Unless there is a continuous supply of nutrients, the lock-up process must lead to a decrease in available minerals. WHITMAN (1974, 1976) observed this process in water level stabilized marshes similar to the one studied in the present paper, where in a relatively short period of time after impounding and flooding the amount of available nutrients declined. As was shown by BEAUCHAMP and KEREKES (1980), newly flooded impoundments tend initially to be limited by nitrogen and later on by phosphorus.

In areas where in more or less regular intervals drought periods occur, freshwater marshes tend to undergo cyclic changes (e.g. WELLER and SPATCHER 1965, WELLER 1978, 1982, VAN DER VALK and DAVIS 1978a,b, 1979, VAN DER VALK 1981). During wet periods nutrients are removed from circulation, accumulated and locked-up in surface litter and soil organic matter, during dry periods they are released through decomposition. Due to recurrent drought, prairie marshes in North America are periodically rejuvenated, a complete cycle requiring from 5 to 35 or more years (VAN DER VALK and DAVIS 1978a). WELLER (1982) argues that natural fires must have occurred regularly in the prairie eliminating the bulk of accumulated plant material, returning locked-up nutrients into circulation and rejuvenating the marsh in a way very similar to that of drought. Whereas drought periods in cool northern ecosystems are too limited in duration and too infrequent to reverse the lock-up process, recent studies (e.g. TOLONEN 1983) indicate that fire has always been an essential ecological factor in northern latitudes. The marsh studied proved to burn anytime of the year provided the weather was sunny and windy since there was a sufficient quantity of contiguous fuel (surface litter) to permit fire spread even among green Typha stems (KRüSI and WEIN 1988).

The hypothesis that ageing ecosystems can be revitalized through improved nutrient cycling conditions brought about by fire has been termed the "paludification-fire-nutrient release hypothesis" (WEIN 1983), "paludification" or "swamping" being the term proposed by HEILMANN (1966) for the species change associated with the nutrient lock-up process. Up to date, quantitative information and experimental studies concerning the paludification-fire-nutrient release hypothesis are rare. Moreover, there is conflicting opinion as to the degree of revitalization and as to whether paludification is enhanced in moist ecosystems (e.g. HEINSELMANN 1975).

The objective of the present study was to test the paludification-fire-nutrient release hypothesis for a Typha glauca floating mat in a water-level stabilized marsh and to compare the effectiveness of burning with that of draining. In order to get a more precise idea of the extent to which draining and burning affect the nutrient status of the system studied, their impact was compared with that of the application of known amounts of fertilizers viz. (i) nitrogen, (ii) phosphorus, (iii) lime and (iv) nitrogen, phosphorus and lime combined. Burning has been reported to have similar effects on plant growth as liming (FOWELLS and STEPHENSON 1934 cited in RAISON 1979) or as fertilizing with nitrogen and phosphorus (e.g. BURTON 1944, RAISON 1979). Treatment effects were evaluated in terms of phenological and growth characteristics of Typha glauca.

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The Postdoctoral Fellowship awarded by the University of New Brunswick as well as the operating funds provided by the World Wildlife Fund (Canada), the Canadian Sportsmen's Fund, Ducks Unlimited (Canada), the Canadian Wildlife Service, the Natural Sciences and Engeneering Research Council of Canada and the University of New Brunswick Research Fund are gratefully acknowledged. Last but not least, statistical analysis of the data would not have been possible without the permission to use the computing facilities at the Centre National Universitaire Sud de Calcul, Montpellier, France, generously granted by the Module "Dynamique et Succession" of the Centre Louis Emberger, Centre National de la Recherche Scientifique, during a stage in 1984 at Montpellier, France.

2. STUDY AREA DESCRIPTION

The study area was established at the head of the Bay of Fundy (New Brunswick, Canada) in the 100 ha Hog Lake Impoundment (45°56' N, 64°17' W); the site is part of the Tintamarre National Wildlife Area and is located about 12 km from Sackville, New Brunswick (Figs. 1 and 2). The general climatic conditions of the area are presented in Figure 3. Daily temperatures and rainfall measured on the site during 1982 are given in Figure 4, the mean chemical composition of the water in the impoundment during 1981 in Table 1.

Although some of the lower tidal wetlands in this area were dyked in the early 1600's, it was not until the 1800's that the present freshwater

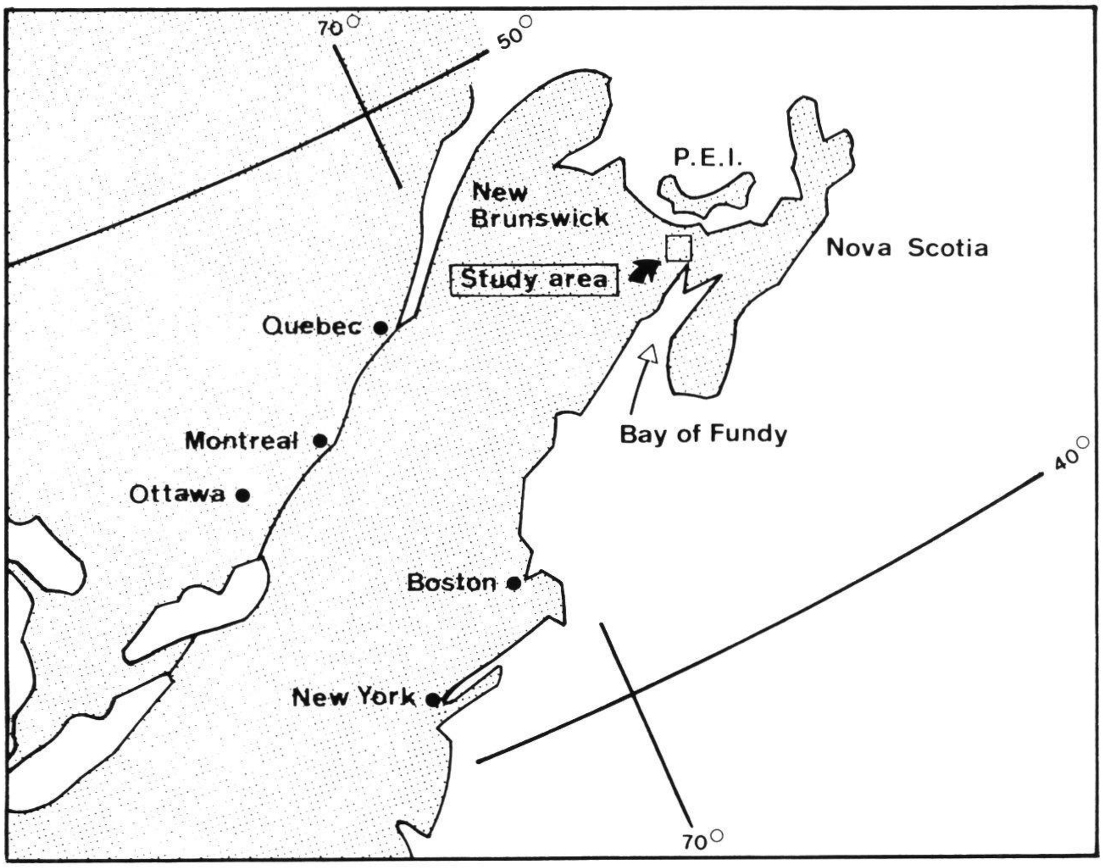


Fig. 1. Location of the study area: Map of Atlantic Canada showing the location of the study area near Sackville, New Brunswick, at the head of the Bay of Fundy.

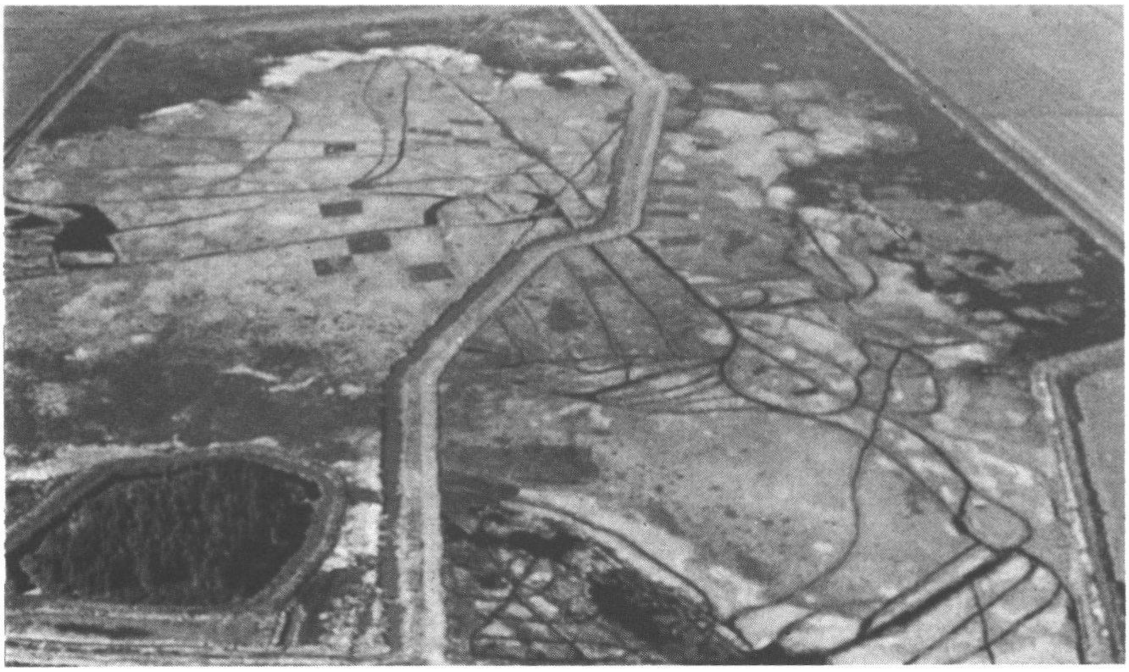


Fig. 2. Aerial view of the study area: The photograph shows the Hog Lake Impoundment in 1981, with the central dyke dividing the impoundment into an undrained (on the right hand side) and a drained basin (on the left hand side). The "trails" were mechanically cut through the floating mat to improve the area for waterfowl. Rectangular dark areas are burned plots.

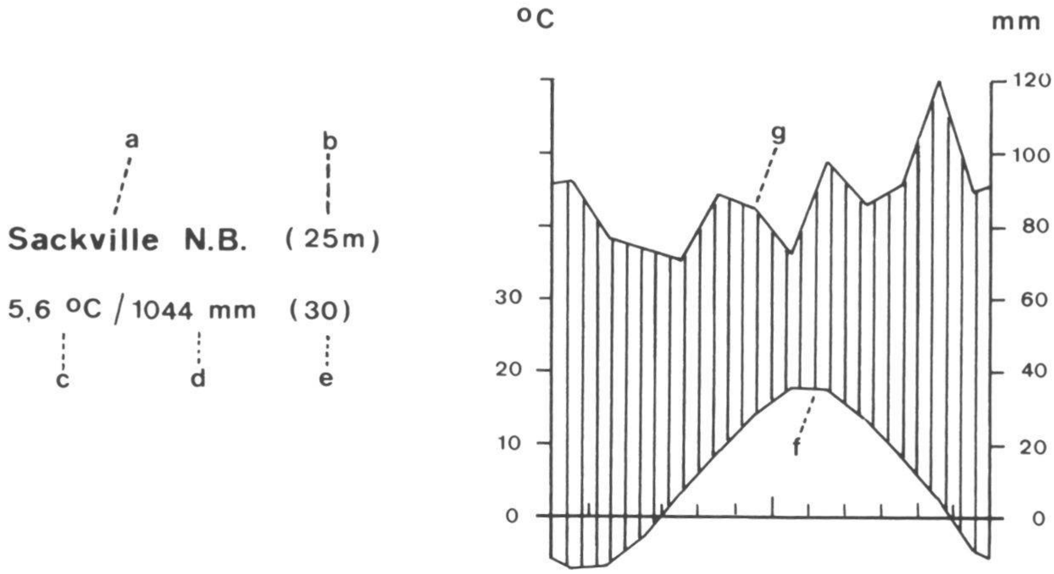


Fig. 3. Climatic diagram of Sackville, New Brunswick, 1941-1970. (Data from ENVIRONMENT CANADA 1975)
a: station; b: height above sea level; c: mean annual temperature (°C); d: mean annual precipitation (mm); e: observation period (years); f: curve of mean monthly temperature; g: curve of mean monthly precipitation. Ordinate: one division = 10°C or 20 mm of rain. Abscissa: months (January-December).

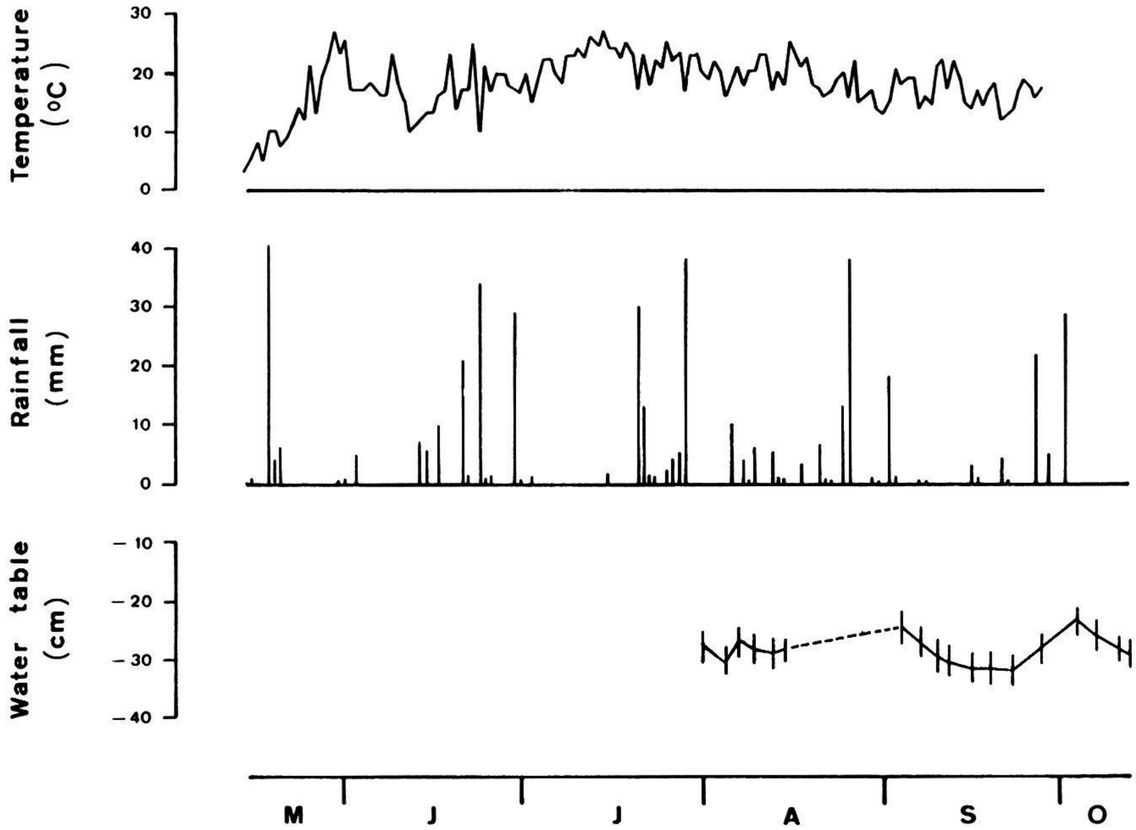


Fig. 4. Temperature, rainfall and water level at the site in 1982: Daily temperatures at 1400 hours, rainfall per 24 hours at the study site and mean (n=8) and standard error of the location of the water table in the drained basin during the vegetation period of 1982.

Table 1. Mean chemical composition of the water in the impoundment studied, during the summer 1981 (from LAKSHMINARAYANA and RIOUX 1982).

* Near the mat surface the pH of the water ranged from 6.2 to 4.8 on Typha-dominated mats and from 4.9 to 3.9 in areas where the successional trend towards poor fen had already progressed (HOGG and WEIN 1988a).

Parameter	ppm	Parameter	ppm
Dissolved oxygen	5.3	Magnesium	8.3
Carbon Dioxide	10.1	Sodium	26.2
Total residue	182.8	Potassium	2.1
Total suspended residue	28.4	Chloride	70.4
Total filtrable residue	154.4	Sulfate	7.5
pH	6.5*	Ortho-phosphate	0.2
Alkalinity (CaCO2)	52.5	Silica	3.9
Hardness (CaCO3)	39.6	COD	56.1
Calcium	3.4		

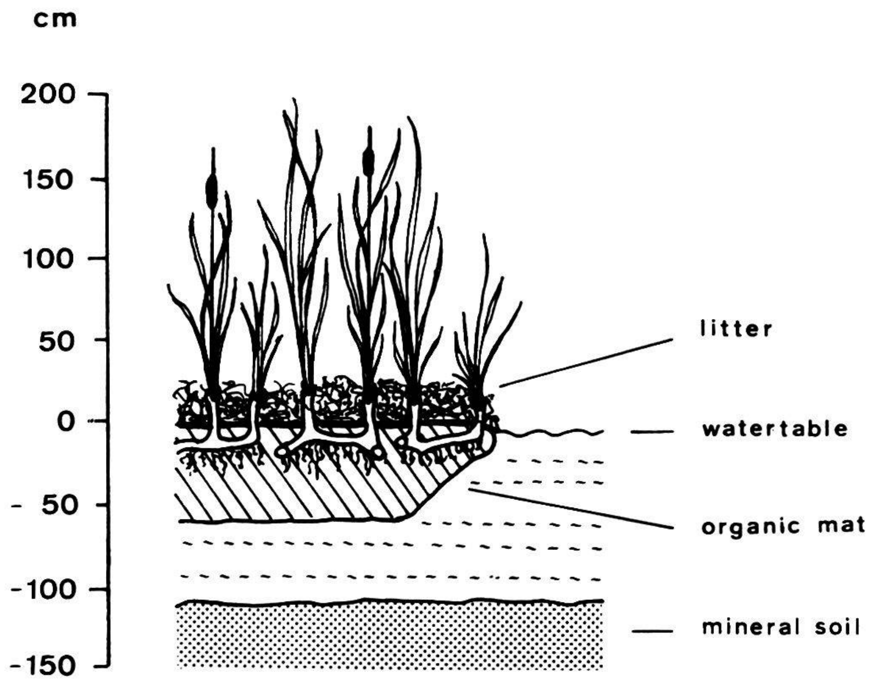


Fig. 5. Schematic profile of the floating mat in the undrained basin.

study site was drained for pasture and hay production. The widespread mechanization of agriculture in the 1950's has made these areas much less attractive for agricultural activities. In the mid-1960's the Canadian Wildlife Service and the Province of Nova Scotia began to acquire some of these unused wetlands as wildlife management areas.

In 1973, the impoundment was dyked on four sides and a water control structure was installed. The site was dominated to some extent by Typha glauca Bodr., a robust hybrid between T. latifolia L. and T. angustifolia L., before the dyking, and after the water level was raised to approximately 1.0 to 1.2 m by snowmelt and rainfall, the Typha mat vegetation floated to the surface and began to expand (Fig. 5). For additional information on the study area, the composition of the floating mat and the mechanism of buoyancy see HOGG and WEIN (1987, 1988a,b).

3. MATERIALS AND METHODS

3.1. EXPERIMENTAL DESIGN

The experimental design was that of a split plot experiment with five replications (blocks) in two locations (e.g. FEDERER 1955); the two locations were the undrained and the drained basin of the impoundment and were considered in the statistical analysis as the only ones of interest. Each block, 9x20 m in size, was divided into two main plots, 4x20 m each, separated from each other by a 1 m wide walkway. The two burning treatments viz. (i) unburned and (ii) burned were assigned randomly to the two main plots. Each main plot, in turn, was then split into five split plots, 4x4 m each, to which the five following fertilizer treatments were allocated at random: (i) no fertilizer added, control (C); (ii) addition of 200 kg/ha actual nitrogen in the form of ammonium-nitrate (N); (iii) addition of 200 kg/ha actual phosphorus in the form of triple superphosphate (P); (iv) addition of 625 kg/ha agricultural grade lime (L); and (v) combined addition of nitrogen phosphorus and lime at above rates (NPL) (Fig. 6). Within every split plot a 0.5x0.5 m quadrat was systematically chosen and permanently marked.

3.2. DRAINING TREATMENTS

The impoundment was drained in mid-November 1980 and a central dyke was constructed during December of the same year, dividing the impoundment into two roughly equal basins. The water control structure on the west basin was closed in February 1981 and due to snowmelt and spring rains the water table reached its original level in that basin by May 1981. In the east basin, on the other hand, the water control structure remained open and drainage continued through 1981 to 1983 (Fig. 2).

Between August 1 and October 12, 1982, the mean water level of eight measuring stations in the drained basin was on the average of 17 measuring days at 28.4 ±0.6 (1 S.E., n = 17) cm below the soil surface with a range from 23.0 ±2.5 (1 S.E., n = 8) cm to 31.6 ±2.5 cm (Fig. 2). By contrast, in the undrained basin the water table remained constantly at the surface of the floating mat (Fig. 5).

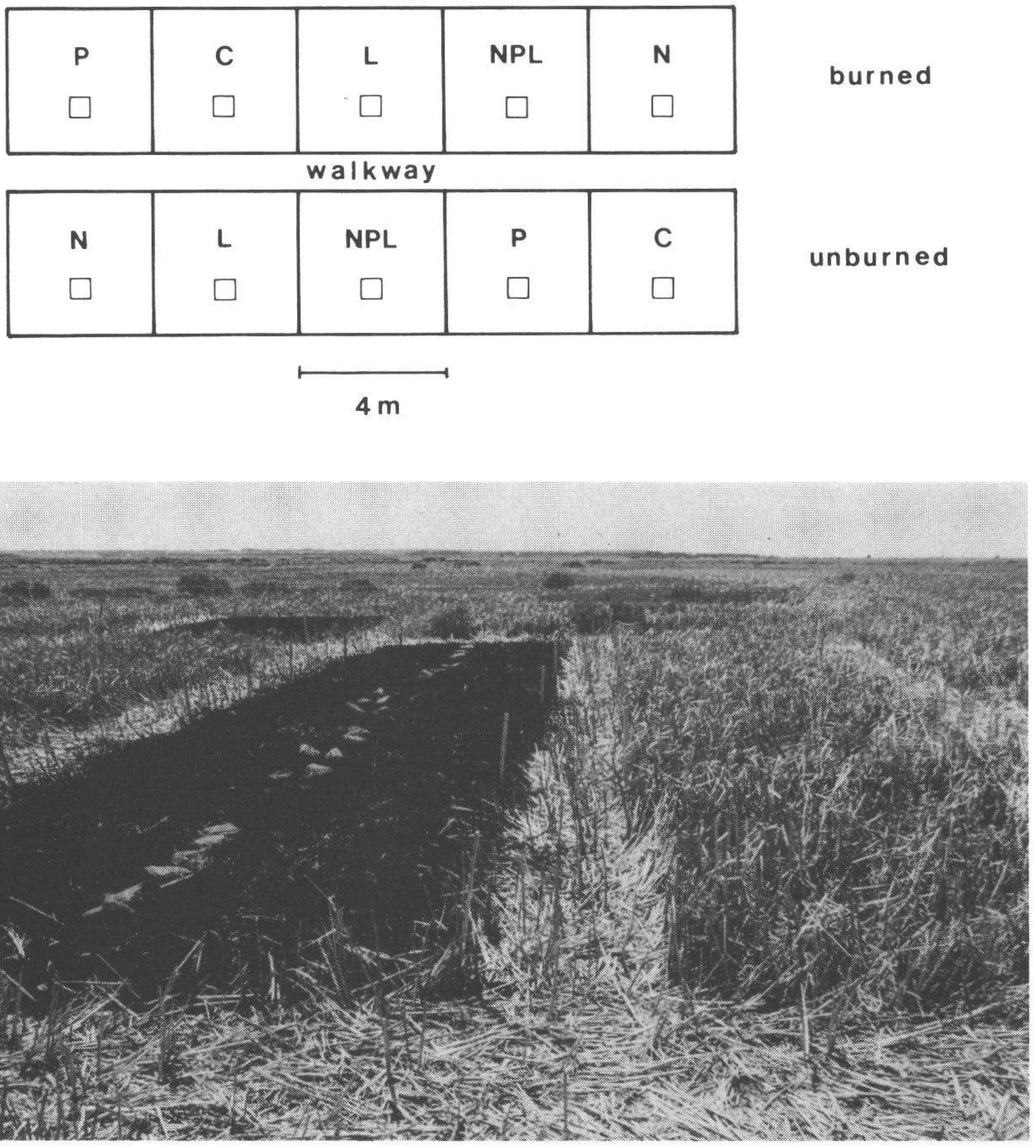


Fig. 6. Experimental design.
Top: Layout of one of the ten blocks. Burning treatments were the main plot treatments and fertilizer treatments the split plot treatments. The small quadrats within the split plots represent the permanently marked 0.5 x 0.5 m plots. C: no fertilizer added; N: 200 kg/ha nitrogen added; P: 200 kg/ha phosphorus added; L: 625 kg/ha lime added; NPL: nitrogen, phosphorus and lime added at above rates. **Bottom:** One of the blocks immediately after burning. In the burned part the bags used for studying the decomposition of surface litter can be seen.

3.3. BURNING AND FERTILIZER TREATMENTS

Burning was carried out on June 3, 1982. The low intensity fires consumed most of the above-ground material but did not penetrate into the organic soil. The above-ground material consisted at the time of burning mainly of surface litter, only few new shoots had already emerged and they were still small. Due to a short residence time of the fire coupled with the high moisture content of the mat, the heat penetrated only into the uppermost centimeters of the mat. The rhizomes of _Typha glauca_ located at a mean depth of 11.6 ±0.35 (1 S.E., n = 118) cm were, thus, well protected from the heating effects.
Burning was carried out in spring for three reasons. First, at that time of year fire does not inflict any severe direct damage to _Typha_ as does, for instance, burning in summer (KRüSI and WEIN 1988). Second, nutrients released by burning are most likely not lost through leaching or surface run-off since at that time _Typha_ starts to grow and can immediately use the available nutrients for biomass production. Finally, marsh fires are most frequent in springtime.
Fertilizer treatments were carried out on June 13, 1982. Fertilizer was applied by hand. The split plots subjected to the different fertilizer treatments were not isolated from each other by any devices, since horizontal water movements within the mat were expected to be negligible. The sharp boundaries of the nitrogen fertilized split plots, which were easily recognizable later in the year due to the dark green colour of the _Typha_ plants growing there, substantiated the assumption.

3.4. MEASUREMENTS

3.4.1. Analytical phenological diagram

Phenological observations for _Typha glauca_ were carried out weekly from late May through November 1982. On the whole, six different developmental stages were distinguished viz. (i) shoots present, (2) staminate spike visible, (3) shedding of pollen, (4) fruit set, (5) yellowing of leaves and (6) seed dispersal. Since the vast majority of the plants did not produce seed heads, the generative development was not studied in greater detail. Every week, the percentage of individuals at a particular phenological phase was estimated using a six-degree scale (+: 0-5%, 1: 5-20%, 2: 20-40%, 3: 40-60%, 4: 60-80%, 5: 80-100%).

3.4.2. Shoot emergence

Since shoot emergence started between two and four weeks before recording of growth parameters was initiated on June 12, the dates on which the first shoots emerged in the different 0.5x0.5 m permanent quadrats had to be assessed indirectly. The respective dates were determined for each unburned 0.5x0.5 m quadrat by extrapolating visually the shoot height vs. date curve backwards (Fig. 7). Estimation of the start of shoot emergence was not possible for the burned treatment plots since burning was carried out before recording of shoot height was initiated.

3.4.3. Shoot density, shoot height, basal shoot circumference and number of leaves per shoot

Number of shoots, total height and height of the green portion, later on referred to as "green height", of all the *Typha* shoots within the permanently marked 0.5x0.5 m quadrats (Fig. 6) were recorded weekly until mid-August and then biweekly. Recording was initiated on June 12 and terminated by October 18. Based on these data it was possible to describe the development of mean shoot density and mean plant height throughout the vegetation period. The final shoot density was defined as the mean number of shoots per square meter recorded during the period from August 6 to October 3, 1982. Preliminary sampling showed that the 0.5x0.5 m shoot density data had to be multiplied by 4 and divided by 1.162 in order to eliminate a systematic error (edge effect) and to make them comparable to values obtained using 1x1 m quadrats. As regards final mean shoot height, October 3 data were used. Basal shoot circumference and number of leaves per shoot were recorded between September 5 and 9, 1982.

3.4.4. Assimilation period

Length of assimilation period was expressed in two ways viz. (i) as "Assimilation period 0%" and (ii) as "Assimilation period 50%" (Fig. 7). Assimilation period 0% was defined as the time in days between the date when in spring the green shoot height was for the last time zero (0% of final shoot height) and the date in autumn when it became for the first time zero again. The respective dates were defined as the intersection of the green shoot height vs. date curve with the abscissa, and were determined for each 0.5x0.5 m permanent quadrat by visual extrapolation of the curve (Fig. 7). In the burned treatment plots, assimilation period

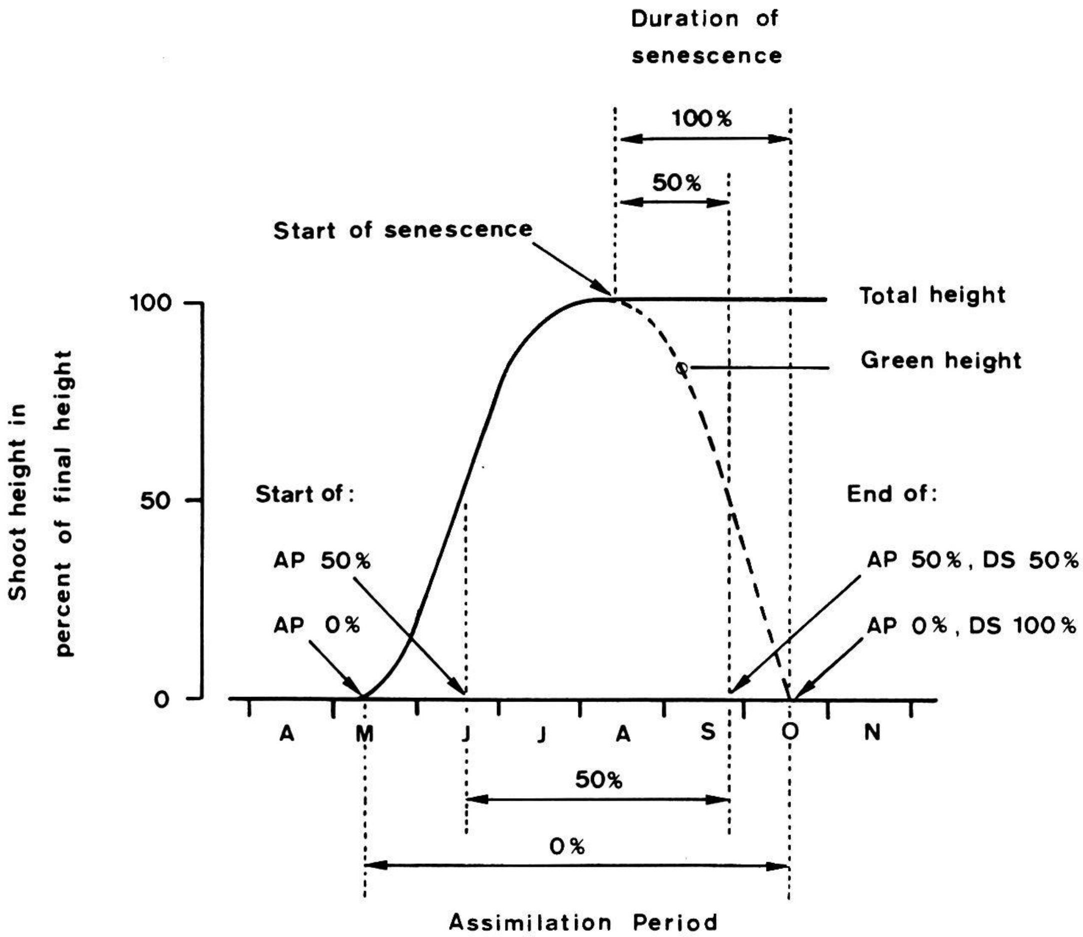


Fig. 7. Definitions of assimilation period and duration of senescence: Schematic diagram illustrating the definitions of start, duration and end of the "Assimilation period 0%" (AP 0%) and the "Assimilation period 50%" (AP 50%) as well as of the start of senescence and the "Duration of senescence 50%" (DS 50%) and the "Duration of senescence 100%" (DS 100%).

0% was considered to have started on or after the day of burning, growth before that date not being taken into account since fire destroyed practically all the shoots that had already emerged at the time.
Assimilation period 50% was defined as the time in days between the date when the height of the green shoot portion rose above and fell below 50% of the final shoot height. The respective dates were determined for each 0.5x0.5 m permanent quadrat by linear interpolation. It is argued that the assimilation period 50% represents the period of time during which the main bulk of photosynthesis is accomplished and reserves are built up in the rhizomes; in early spring, when shoots have not yet reached 50% of their final height, growth depends largely on rhizome reserves and in autumn, when the height of the green shoot portion has fallen below the 50% mark, the assimilating surface is too limited to increase substantially the amount of reserves built up during the vegetation period.

3.4.5. Senescence

The start of senescence was defined as the date on which the process of progressive yellowing of leaves commenced. The onset of progressive yellowing did not differ among the treatments: in all the plots, senescence started on the same day, i.e. August 14. Duration of senescence was defined as the period of time in days between the start of progressive yellowing, i.e. August 14, and the day on which the senescence process was complete to 50% (duration of senescence 50%) and to 100% (duration of senescence 100%), respectively. The senescence process was considered to be halfway through on the day on which the mean height of the green shoot portion fell below 50% of the total shoot height and considered to be 100% complete on the day on which all the shoots had become entirely brown (Fig. 7). For each 0.5x0.5 m permanent quadrat, the respective dates were determined visually on the shoot height vs. date graph (Fig. 7). The two measures, duration of senescence 50% and duration of senescence 100%, allow to estimate the rate of the senescence process in the different draining, burning and fertilizer treatments.

3.4.6. Susceptibility to drought and insect damage

Susceptibility to drought was quantified by measuring the length on which the leaves died back during periods of low rainfall; leaf die-back was expressed in percent of total shoot height at the time of recording. The percentage of shoots attacked by stem boring insect larvae was recorded on August 6 and September 3; the mean of the two sampling dates was used for analysis.

3.4.7. Standing crop

Above-ground standing crop was sampled in C- and NPL-plots only. In late October and early November, within each of these plots one 0.5x0.5 m quadrat was chosen at random, the above-ground biomass was cut at ground level, separated into (i) current year's (1982) *Typha* growth, (ii) current year's growth of plants other than *Typha* and (iii) litter. Samples were dried at 100 $^{\circ}C$ to constant weight. For the fertilizer treatments, where above-ground standing crop was not measured, current year's *Typha* shoot standing crop (S) was estimated for every treatment plot with help of multiple regression, using the means of final shoot height (H), final shoot density (D), basal shoot circumference (C) and number of leaves per shoot (L) as predictor variables; the regression equation was $\ln(S) = -7.5417 + 1.2549*\ln(H) + 0.9624*\ln(D) + 1.4997*\ln(C) - 0.8836*\ln(L)$ (r-square = 0.952). *Typha* shoot standing crop on June 19 (SJ) was estimated using the means of shoot height (HJ) and shoot density (DJ) at that date as predictor variables; the regression equation was $\ln(SJ) = -9.2629 + 2.4953*\ln(HJ) + 0.9368*\ln(DJ)$ (r-square = 0.949).

3.5. STATISTICAL PROCEDURES

Multiple regression was calculated in the logarithmic scale (natural logarithms), using PROC STEPWISE and PROC REG of the Statistical Analysis System (S.A.S. Institute 1982), and differences between draining, burning and fertilizer treatments were determined by analysis of variance

Table 2. Transformations used to make data appropriate for analysis of variance.

Variable	Transformation
- Start of shoot emergence	-
- Shoot density on June 12	logarithmic
- Shoot density on June 19	square root
- Shoot density on June 19 in percent of final shoot density	angular (arcsin $\sqrt{x}$)
- Final shoot density	square root
- Shoot height on June 19	-
- Final shoot height	x**1.57
- Basal shoot circumference	logarithmic
- Number of leaves per shoot	-
- Length of the assimilation period 0%	-
- Length of the assimilation period 50%	x**1.57
- Start of the assimilation period 0%	-
- Start of the assimilation period 50%	-
- Day after May 15 on which shoot height reached 71.1 cm	square root
- Duration of senescence 50%	-
- Duration of senescence 100%	-
- Green height in percent of total height on October 3	angular (arcsin $\sqrt{x}$)
- Susceptibility to drought (percent leaf die-back on June 19	angular (arcsin $\sqrt{x}$)
- Insect damage (percent infested shoots)	angular (arcsin $\sqrt{x}$)
- *Typha* shoot standing crop on June 19	logarithmic (ln(x+1))
- *Typha* shoot standing crop in Oct./Nov.	logarithmic
- Standing crop of plants other than *Typha* in Oct./Nov.	logarithmic
- Litter load in Oct./Nov.	logarithmic

with help of PROC GLM. The transformations used to make the data meet the assumptions of the analysis of variance are summarized in Table 2. Tests of significance were performed on the transformed data but means are reported in the untransformed scale; the means reported in the untransformed scale were also calculated in this scale and not back-transformed. When for a parameter more than one value per permanent 0.5x0.5 m quadrat was recorded, as was the case for final shoot density, shoot height, basal shoot circumference, number of leaves per shoot and percent leaf die-back, the means were used for analysis of variance. Analysis of variance was calculated for the entire data set (all four draining x burning regimes combined) as well as separately for the two draining (burning treatments combined) and the two burning (draining treatments combined) regimes. The fertilizer treatment sums of squares were decomposed into the four following planned orthogonal comparisions: C vs. NPL, C vs. N, C vs. P and C vs. L. Unplanned multiple comparisons between pairs of fertilizer treatment means were tested according to the T-method, and unplanned contrasts among fertilizer means according to SCHEFFE's method (SOKAL and ROHLF 1981). Tests of significance within a single draining x burning regime were made using the pooled error mean square of the two burning treatments in the respective draining regime.

4. RESULTS

The results are arranged according to the different phenological and growth parameters of Typha glauca measured. First, the general phenological development of Typha is described as observed during 1982 under undisturbed conditions in the undrained basin (Fig. 8). Then, for each of the parameters studied, the effects of draining, burning and fertilizing are discussed. An overview over the variables considered, their response to the treatments and the results of the analysis of variance tests are given in Table 3.

4.1. GENERAL PHENOLOGICAL DEVELOPMENT OF TYPHA

Growth commenced in late May and by mid-July most of the shoots had emerged (Fig. 8). By mid-August leaves started to turn yellow at the tips. Senescence proceeded slowly throughout September, became much more

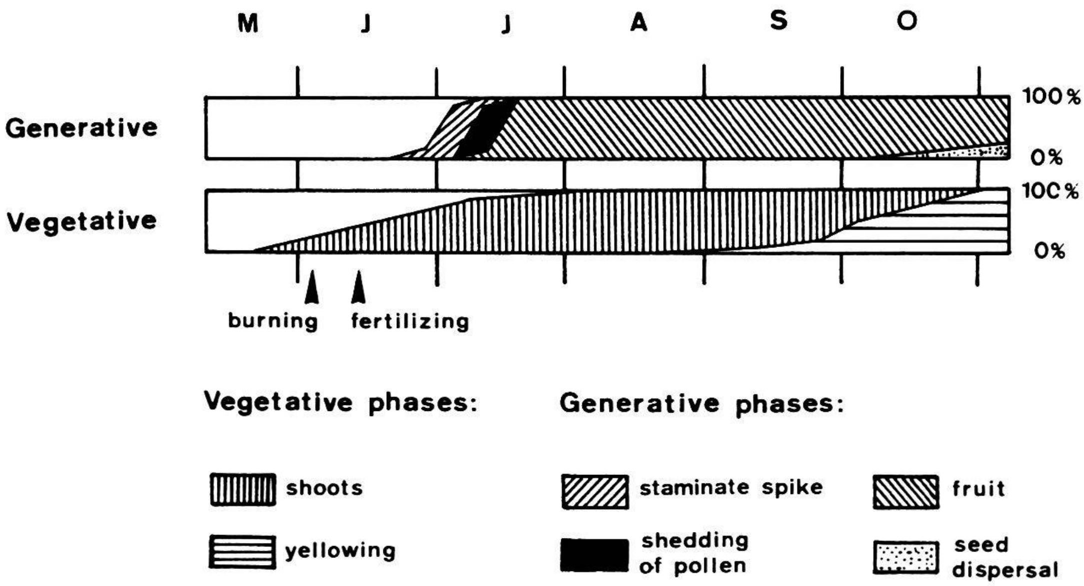


Fig. 8. General phenological development of Typha glauca during 1982 on unburned and unfertilized plots in the undrained basin.

Table 3. Results of analysis of variance tests in an experiment comparing the effects of draining, spring burning and different fertilizer treatments on phenological and growth parameters of *Typha glauca* in New Brunswick, Canada.

	Start of shoot emergence	Shoot density on June 12	Shoot density on June 19	Shoot density on June 19 in % of final shoot density	Final shoot density	Shoot height on June 19	Final shoot height	Basal shoot circumference	Number of leaves per shoot	Length of the assimilation period 0%	Length of the assimilation period 50%
Both draining treatments combined											
Draining (D)	***	***	**	*	NS	***	*	*	NS	***	***
Burning (B)	-	**	NS	NS	NS	***	(*)	NS	NS	***	**
Fertilizing (F)	-	-	NS	(*)	NS	NS	***	***	***	***	***
C vs. NPL	-	-	NS	NS	NS	NS	***	***	***	**	NS
C vs. N	-	-	NS	NS	NS	NS	***	***	***	***	***
C vs. P	-	-	(*)	NS	NS	NS	NS	NS	NS	NS	NS
C vs. L	-	-	NS	NS	NS	NS	NS	NS	NS	NS	NS
D x B	-	*	NS	NS	NS	NS	NS	NS	NS	**	*
D x F	-	-	NS	*	NS	NS	NS	NS	(*)	NS	NS
B x F	-	-	NS	NS	NS	NS	NS	NS	*	NS	NS
Undrained treatments only											
Burning (B)	-	NS	NS	NS	NS	**	NS	NS	NS	***	*
Fertilizing (F)	-	-	NS	**	NS	NS	***	***	**	***	**
C vs. NPL	-	-	NS	**	NS	NS	***	***	***	**	NS
C vs. N	-	-	NS	**	NS	NS	*	***	*	***	***
C vs. P	-	-	NS	NS	NS	NS	NS	NS	NS	(*)	NS
C vs. L	-	-	NS	NS	NS	NS	NS	NS	NS	NS	NS
B x F	-	-	NS	NS	NS	NS	*	NS	NS	NS	NS
Drained treatments only											
Burning (B)	-	**	NS	NS	NS	*	NS	NS	NS	NS	NS
Fertilizing (F)	-	-	NS	NS	NS	NS	***	***	***	*	*
C vs. NPL	-	-	NS	NS	NS	NS	***	***	***	NS	NS
C vs. N	-	-	NS	NS	NS	NS	**	***	***	NS	*
C vs. P	-	-	NS	NS	NS	NS	NS	NS	NS	NS	NS
C vs. L	-	-	*	*	NS	NS	NS	NS	NS	NS	NS
B x F	-	-	NS	NS	NS	NS	NS	NS	NS	NS	NS

Table 3. (continued)

Fertilizer treatments:
C no fertilizer added, control
N nitrogen added (200 kg/ha)
P phosphorus added (200 kg/ha)
L lime added (625 kg/ha)
NPL nitrogen, phosphorus, and lime added at above rates

Significance symbols:
(*) P<0.06
* P<0.05
** P<0.01
*** P<0.001
NS P>0.06
- no measurements

	Start of the assimilation period 0%	Start of the assimilation period 50%	Day after May 15 on which shoot height reached 71.1 cm	Duration of senescence 50%	Duration of senescence 100%	Green height in percent of total height on October 3	Susceptibility to drought (% leaf die-back on June 19)	Insect damage (% infested shoots)	Typha shoot standing crop on June 19	Typha shoot standing crop in October/November	Standing crop of plants other than Typha in October/November	Litter load in October/November
Both draining treatments combined												
Draining (D)	***	***	***	***	***	***	***	***	***	**	*	NS
Burning (B)	***	***	***	**	*	*	*	**	**	NS	**	***
Fertilizing (F)	-	**	*	***	***	***	***	NS	NS	***	NS	NS
C vs. NPL	-	***	(*)	***	***	***	***	NS	NS	***	NS	NS
C vs. N	-	NS	**	***	***	**	NS	NS	NS	***	-	-
C vs. P	-	NS	NS	NS	NS	NS	***	NS	(*)	NS	-	-
C vs. L	-	NS	NS	NS	(*)	NS	NS	NS	NS	NS	-	-
D x B	**	NS	NS	NS	NS	NS	*	*	NS	NS	***	**
D x F	-	NS	NS	NS	NS	(*)	***	NS	NS	NS	*	NS
B x F	-	NS	NS	NS	NS	NS	**	NS	NS	NS	NS	*
Undrained treatments only												
Burning (B)	***	**	***	NS	NS	NS	NS	*	*	NS	***	***
Fertilizing (F)	-	(*)	NS	**	***	NS	NS	NS	NS	***	*	NS
C vs. NPL	-	*	NS	**	**	*	NS	NS	NS	***	*	NS
C vs. N	-	NS	*	**	***	NS	NS	NS	NS	**	-	-
C vs. P	-	NS	NS	NS	*	NS	NS	NS	MS	NS	-	-
C vs. L	-	NS	NS	NS	NS	NS	NS	NS	NS	NS	-	-
B x F	-	NS	NS	NS	NS	NS	NS	NS	NS	NS	(*)	NS
Drained treatments only												
Burning (B)	**	**	*	*	(*)	NS	(*)	NS	*	NS	NS	***
Fertilizing (F)	-	*	NS	***	***	***	**	NS	NS	***	NS	NS
C vs. NPL	-	**	NS	**	NS	*	***	NS	NS	***	NS	NS
C vs. N	-	NS	NS	**	NS	*	NS	NS	NS	***	-	-
C vs. P	-	NS	NS	NS	NS	NS	***	NS	NS	NS	-	-
C vs. L	-	NS	NS	NS	*	*	NS	NS	NS	NS	-	-
B x F	-	NS	NS	NS	NS	NS	**	NS	NS	NS	**	NS

rapid with the beginning of October and was completed by the end of that month. The first flower heads became visible on June 22, and shedding of pollen began in the second week of July. Seed dispersal commenced in early October. Approximately 75% of the seed heads had, however, not yet commenced to shed their seed by early November and some of them were still intact the following spring. In the area where the study plots were located, only approximately 1-2% of the *Typha* plants produced seed heads. In a 2 to 5 m wide strip along the drainage channels the percentage of fruiting plants was much higher; here approximately one third of the plants developed seed heads.

4.2. SHOOT DENSITY

4.2.1. Shoot emergence

The start of shoot emergence was significantly delayed by draining. In the drained basin, the first shoots appeared on average 11 days later than in the undrained basin ($P<0.001$) (Figs. 9 and 10, Appendix 1). Burning and fertilizing, on the other hand, could not affect the start of shoot emergence in the present experiment since those treatments were applied only after the first shoots had emerged in most of the treatment plots.

On June 12, that is nine days after burning and one day before fertilizers were applied, shoot density was already significantly higher in burned than in unburned plots (7.0 vs. 4.4 shoots/m^2; $P<0.002$) (Appendix 2). The difference between burned and unburned plots was much more important in the drained (7.0 vs. 1.4 shoots/m^2; $P<0.01$) than in the undrained basin (9.0 vs. 7.4 shoots/m^2; n.s.). It is argued that in the undrained basin fire intensity was too low and shoot emergence already too advanced at the time of burning to be affected by the treatment. The accelerated shoot emergence observed in the burned plots of the drained basin was probably due to improved microclimatic conditions brought about by the fire. On June 12, shoot density in the drained treatments amounted to only 39% of the density found under undrained conditions (3.2 vs. 8.2 shoots/m^2; $P<0.0001$; both burning treatments combined);

fertilizers had not yet been applied by then.

On June 19, that is 16 days after burning and six days after fertilizers had been applied, shoot density was still significantly lower in the drained than in the undrained basin, but the difference had become smaller (Fig. 11, Table 3, Appendix 3). Burning and fertilizer treatments combined, shoot density in the drained treatments amounted now to 68.1% of that observed in the undrained treatments (14.5 vs. 21.3 shoots/m^2; $P<0.01$). Sixteen days after burning the difference between burned and unburned treatment plots had practically disappeared (17.8 vs. 18.0 shoots/m^2). The fertilizer treatments, on the other hand, had already brought about the first effects (Fig. 11).

Global evaluation of the data with no regard to draining and burning treatments showed shoot density to be highest in P- and L-plots with 21.0 and 19.8 shoots/m^2, followed by NPL-, C- and N-treatment plots with 17.2, 16.0 and 15.5 shoots/m^2, respectively; the difference between C- and P-treatments was almost significant (Table 3, $P<0.055$). The impact of phosphorus was very similar in the two draining treatments but somewhat more pronounced in the drained (16.2 vs. 10.7 shoots/m^2 in unfertilized plots) than in the undrained basin (25.8 vs. 21.3 shoots/m^2). By June 19, liming, on the other hand, had not affected shoot density under undrained conditions (22.1 vs. 21.3 shoots/m^2 in unfertilized plots) but had increased it in the drained ones (17.6 vs. 10.7 shoots/m^2; $P<0.05$). Addition of nitrogen alone or in combination with phosphorus and lime, finally had not yet resulted in significant differences, but in the undrained basin shoot density was consistently lower in N- and NPL-plots (17.6 and 19.6 vs. 21.3 shoots/m^2 in unfertilized plots) and in the drained basin consistently higher than in unfertilized plots (13.4 and 14.8 vs. 10.7 shoots/m^2 (Appendix 3).

In order to quantify the extent to which shoot emergence had progressed, shoot density on June 19 was expressed in percent of final shoot density (Figs. 12 and 13, Appendix 4). On June 19, shoot emergence was more advanced in the undrained than in the drained basin. In the undrained treatments already 69.9% of the shoot had appeared as compared to only 57.9% in the drained ones ($P<0.05$; all burning and fertilizer treatments combined). The difference between burned and unburned plots where, on June 19, 60.7 and 67.2%, respectively, of the final density had been reached was, on the other hand, not significant.

As regards the fertilizer treatments, global evaluation of the data

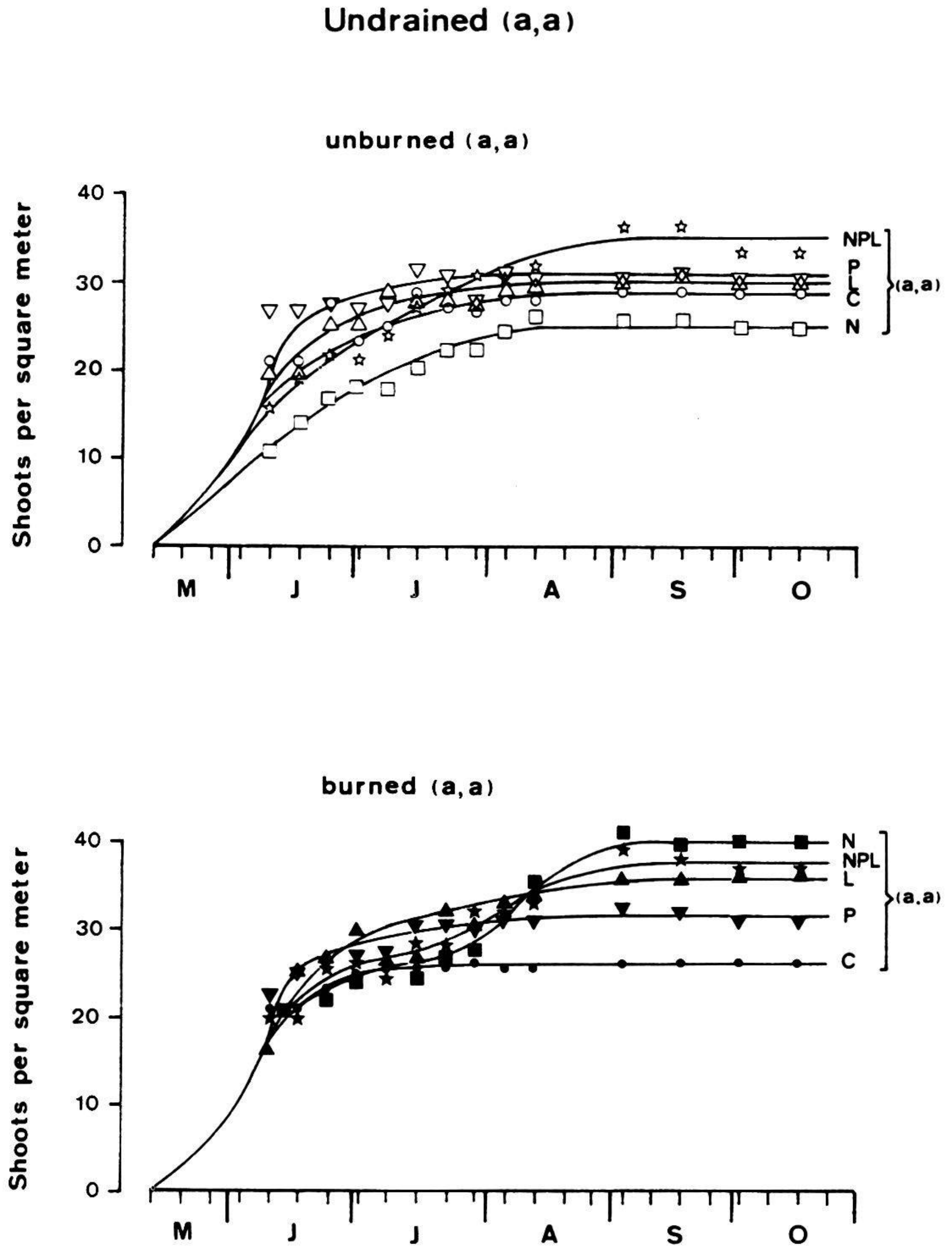


Fig. 9. Development of the shoot density (shoots per square meter) of Typha glauca in unburned (top) and burned (bottom) plots of the undrained basin, on which were superimposed five fertilizer treatments.

C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added. Values are means n = 5. Two burning means (all fertilizer treatments combined, n = 25) and two fertilizer treatment means within a single burning regime (n = 5) sharing the same letter are not significantly different at $P<0.05$. The first letter following the treatment indication refers to the mean shoot density on June 19, the second the final shoot density.

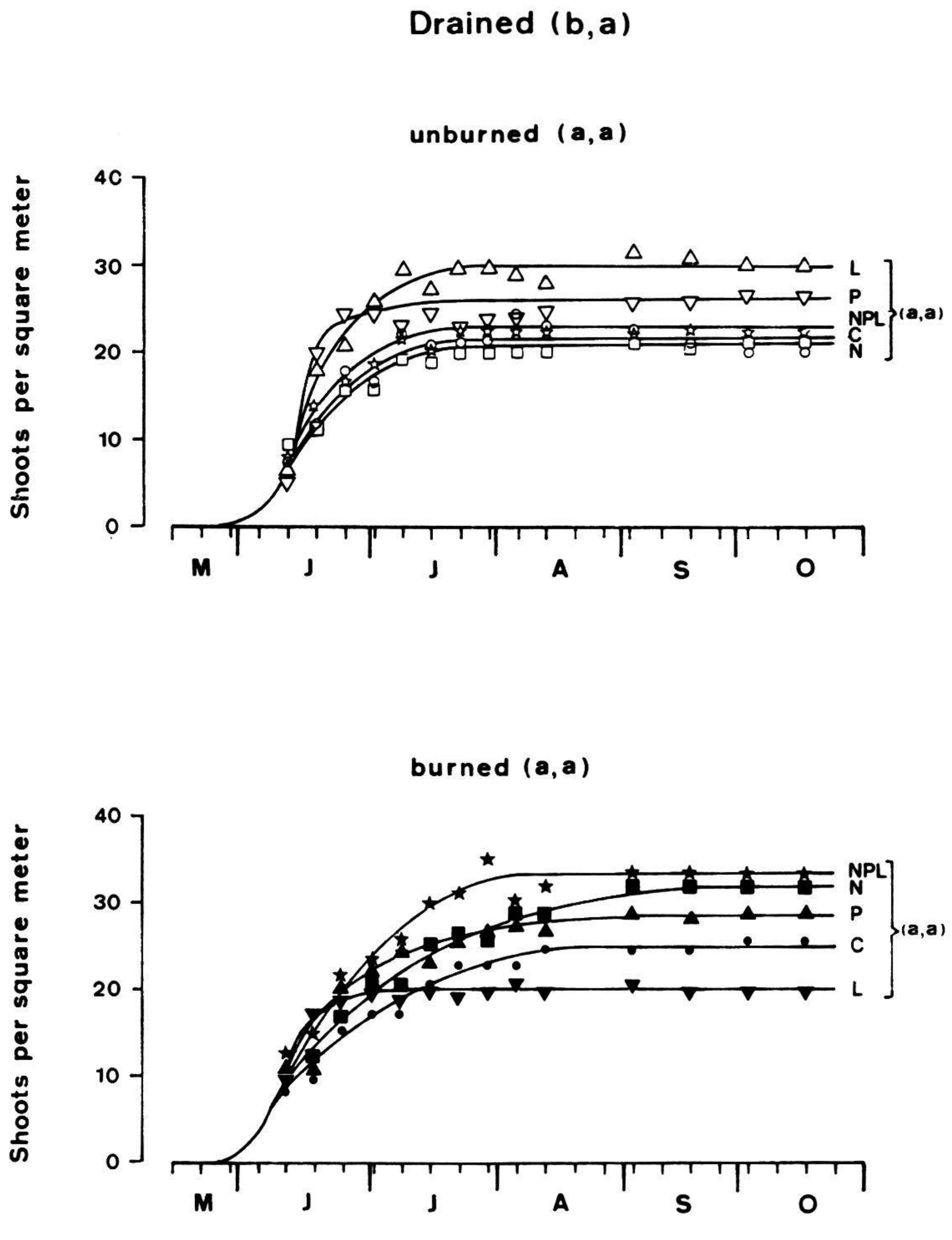


Fig. 10. Development of the shoot density (shoots per square meter) of Typha clauca in unburned (top) and burned (bottom) plots of the drained basin, on which were superimposed five fertilizer treatments.

C: unfertilized; NPL: nitrogen, phorphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added. Values are means n = 5. Two burning means (all fertilizer treatments combined, n = 25) and two fertilizer treatment means within a single burning regime (n = 5) sharing the same letter are not significantly different at $P<0.05$. The first letter following the treatment indication refers to the mean shoot density on June 19, the second to the final shoot density.

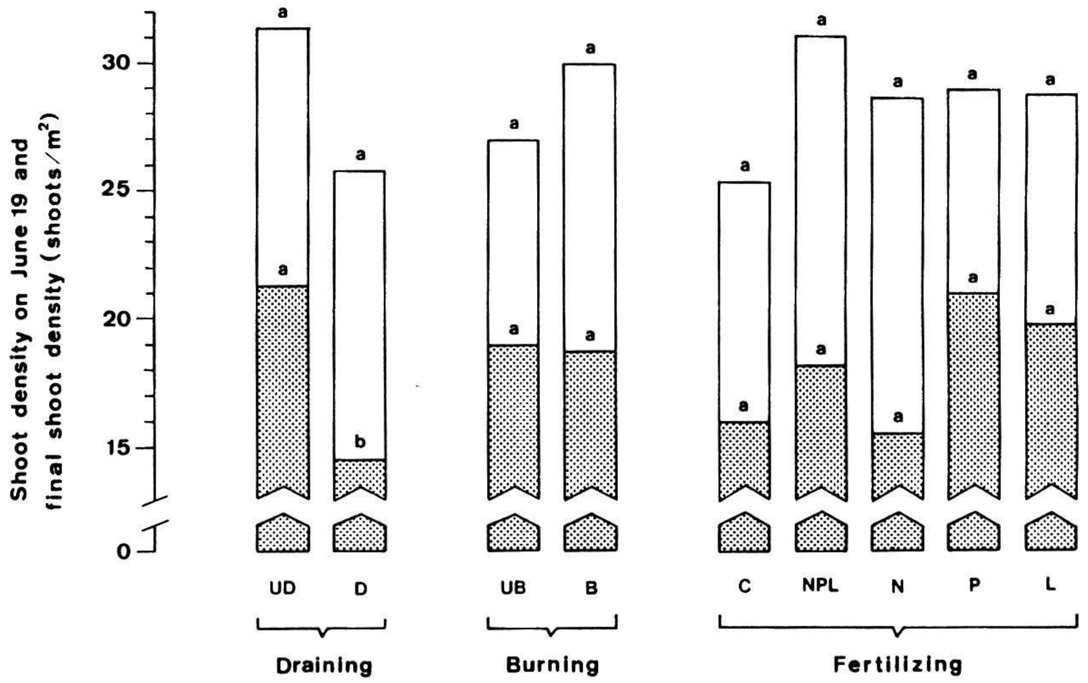


Fig. 11. Shoot density per square meter on June 19 (shaded portion) and final shoot density (entire bars) of Typha glauca under different draining, burning and fertilizer treatments. **Draining treatments:** UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons).

showed almost significant differences among the treatments ($P<0.053$) (Fig. 12, Table 3). Shoot emergence was most advanced in P- and L-treatments with 71.6 and 69.7% of the shoots present, followed by the unfertilized control plots with 63.3%, and lowest in N- and NPL-treatments where so far only 57.4% and 57.5% of the shoots had emerged (Fig. 12, Appendix 4). The contrast between NPL- and N-plots on the one hand and P- and L-treatments on the other hand, was almost significant ($P<0.056$). However, fertilizer impact was not the same in the two draining treatments (draining x fertilizer interaction: $P<0.05$) (Table 3). In the undrained basin, the percentage of shoots present on June 19 was almost consistently lower in fertilized than in unfertilized treatments, the only exception being unburned P-plots (Fig. 13); in the case of the N-

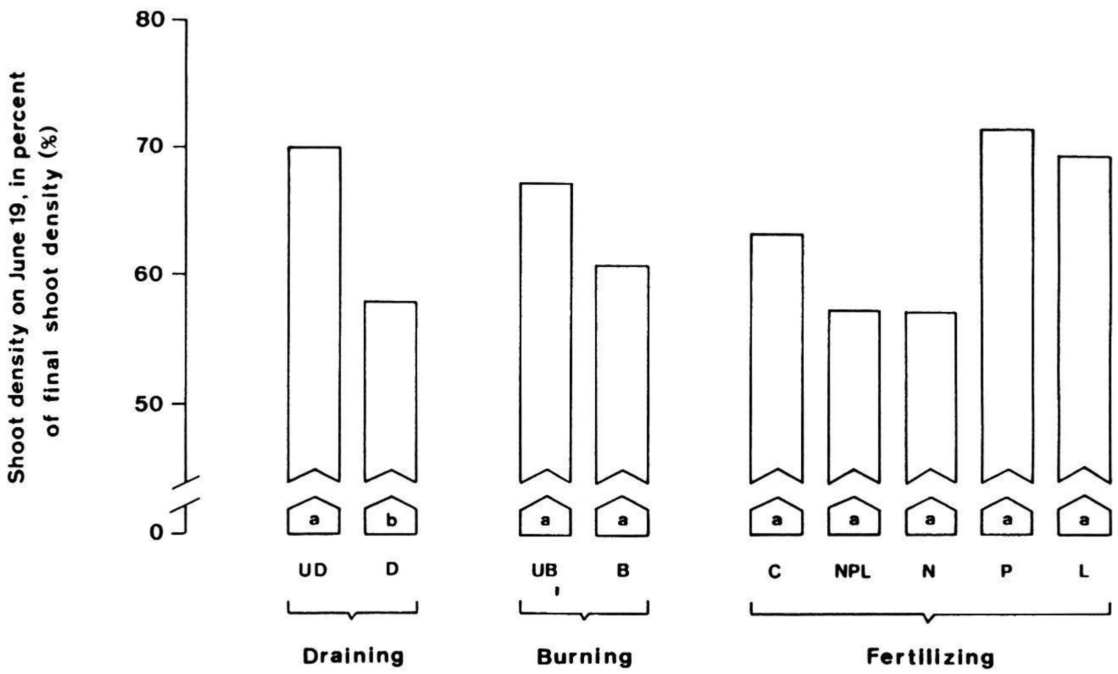


Fig. 12. Shoot density of Typha glauca on June 19, in percent of final density, under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons).

and NPL-treatments, where only 59.0 and 58.6% of the final shoot density had been reached, shoot emergence had significantly less progressed than in unfertilized plots with 79.7 of the shoots present (both $P<0.01$). In the drained basin, in contrast, shoot emergence was always more advanced in fertilized than in unfertilized treatments, the difference between limed and unfertilized plots being significant (69.5 vs. 46.9%; $P<0.05$) (Fig. 13, Table 3, Appendix 4).

All draining x burning regimes combined, shoot emergence was completed first in phosphorus and lime treatments, followed by unfertilized plots and last in NPL- and particularly in N-treatment plots (Figs. 9 and 10).

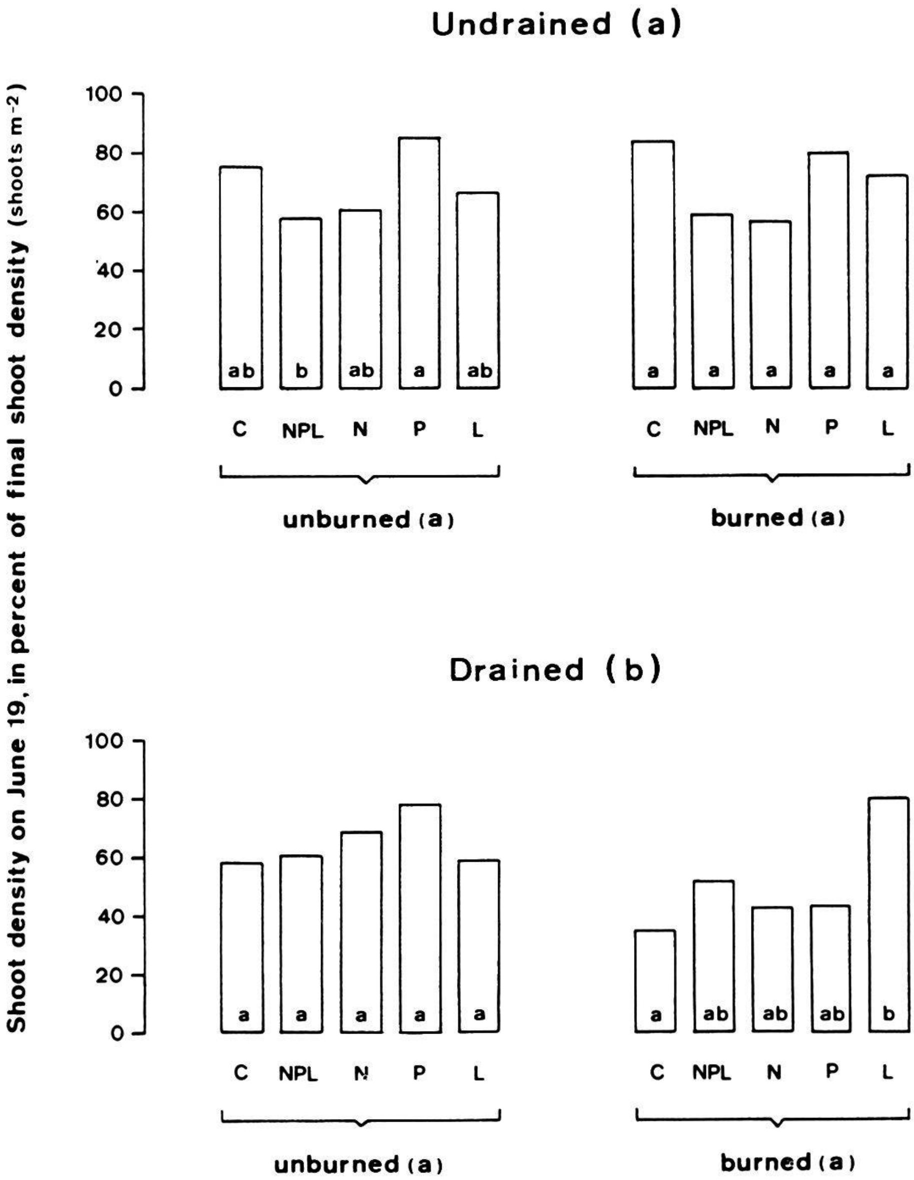


Fig. 13. Shoot density of Typha glauca on June 19, in percent of final density, in response to different fertilizer treatments which were superimposed on four draining x burning regimes. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 5. Two draining means (all burning and fertilizer treatments combined; n = 50), two burning means within a single draining regime (all fertilizer treatments combined, n = 25) and two fertilizer means within a single draining x burning regime (n = 5) sharing the same letter are not significantly different at P<0.05 (unplanned pairwise comparisons).

4.2.2. Final shoot density

Final shoot density did not differ significantly between the draining, burning and fertilizer treatments studied (Table 3). Nevertheless, the differences are sufficiently pronounced that the trends indicated by the data could most likely be corroborated by increasing the number of samples (Fig. 11, Appendix 5).

The data indicate final shoot density to be higher under undrained than under drained conditions (31.3 vs. 25.8. shoots/m^2) but lower in unburned than in burned treatments (27.0 vs. 30.0 shoots/m^2). Global evaluation of the data with no regard to the different draining x burning regimes showed somewhat higher shoot densities in fertilized (N-, P-, L- and NPL-treatments combined) than in unfertilized plots (29.4 vs. 25.4 shoots/m^2). Shoot density was highest in the NPL-treatments (31.1 shoots/m^2), followed by N-, P-, L- and C-plots with 28.7, 29.0, 28.8 and 25.4 shoots/m^2, respectively. Combining N-, P-, L- and NPL-treatments, the sole distinction being made between fertilized and unfertilized plots, fertilizer impact tended to be more pronounced in undrained (32.4 shoots/m^2 in fertilized vs. 27.4 shoots/m^2 in unfertilized plots) than in drained (26.5 vs. 23.3 shoots/m^2) and more important in burned (31.4 vs. 25.2 shoots/m^2) than in unburned (27.3 vs. 25.6 shoots/m^2) treatment plots (Appendix 5).

As regards the draining and burning treatments, the trends indicated by the present data are corroborated by data collected in a different set of plots on the same site (KRÜSI and WEIN 1988) where the shoot density was found to be significantly higher in undrained than in drained ($P<0.001$) and significantly lower in unburned than in burned ($P<0.01$) treatments plots.

4.3. SHOOT HEIGHT

In the drained basin, shoots were significantly smaller than in the undrained basin, both on June 19, and at the end of growth (Table 3, Figs. 14, 15 and 16). On June 19, they were 46.6% smaller in the drained as compared to the undrained treatments (30.8 vs. 57.7 cm; $P<0.0001$; all

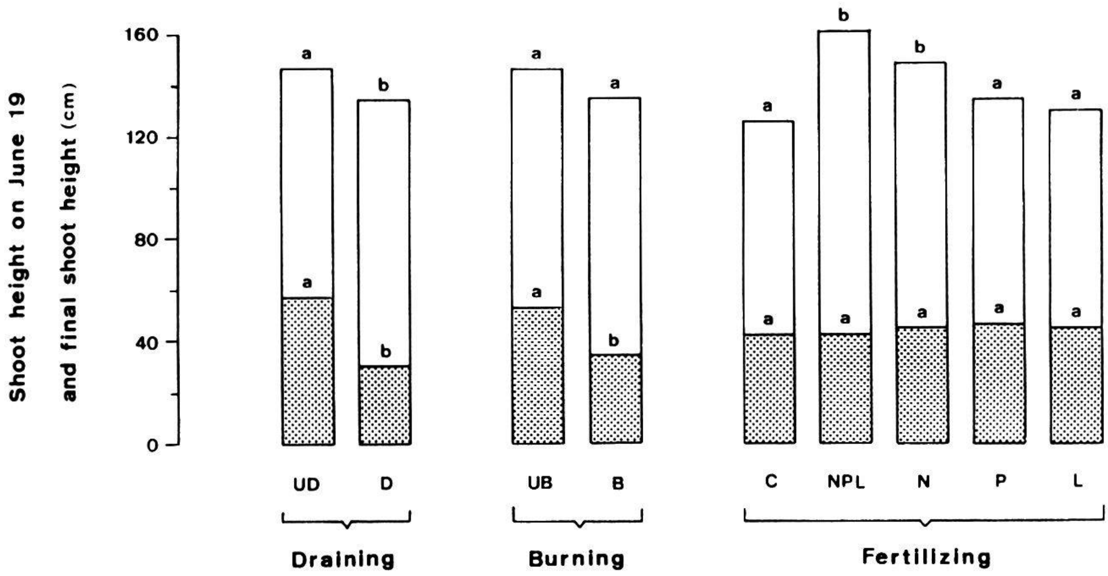


Fig. 14. Shoot height on June 19 (shaded portion) and final shoot height (entire bars) of Typha glauca under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons).

burning and fertilizer treatments combined) and, once they had reached their final height, they were still smaller by 9.4% (133.2 vs. 147.0 cm; $P<0.02$) (Appendices 6 and 7).

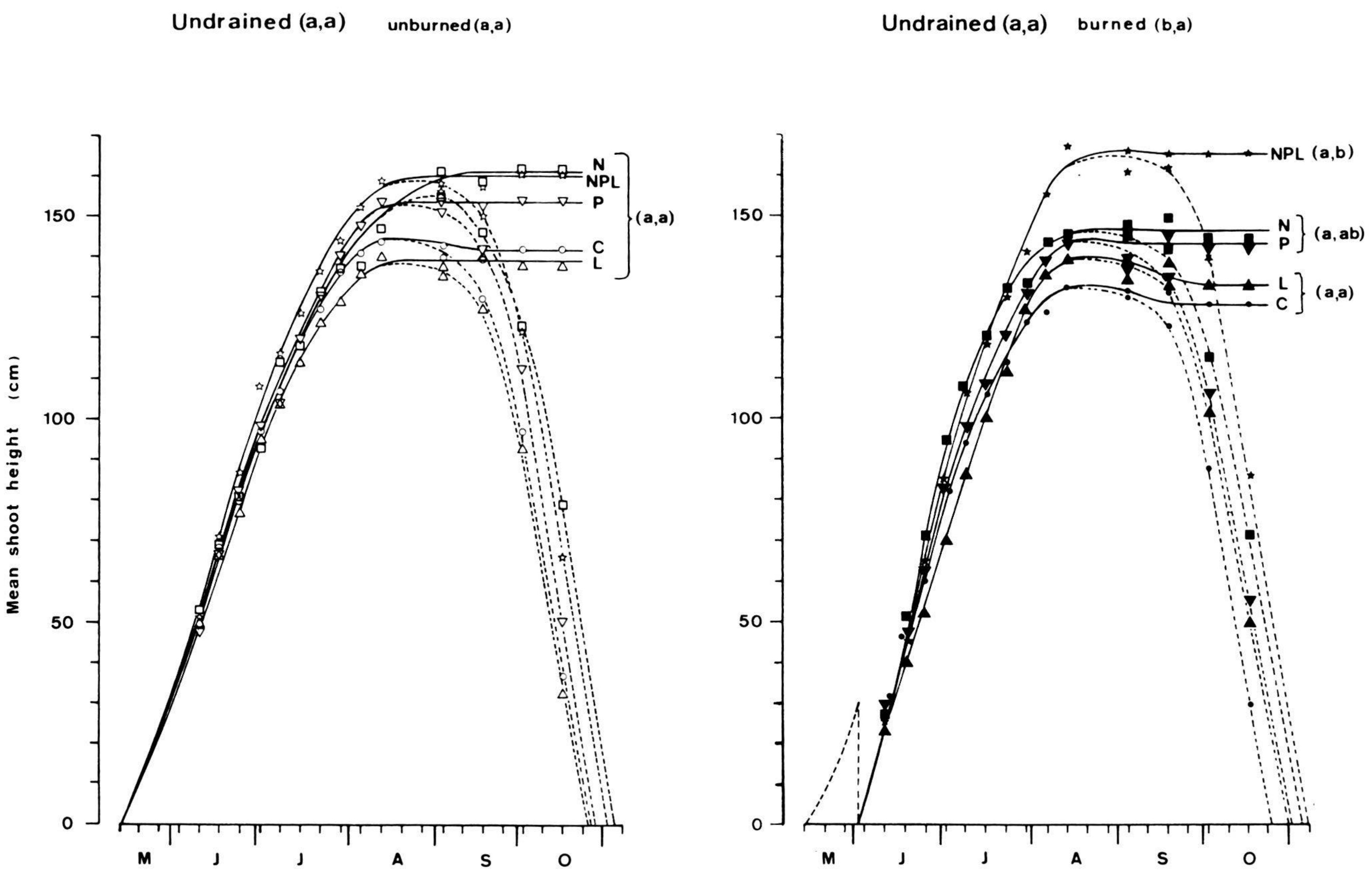
Burning resulted likewise in reduced shoot height (Figs. 14, 15 and 16). On June 19, that is 16 days after the fire, the mean shoot height in burned plots was 33.3% lower than in unburned ones (35.4 vs. 53.1 cm; $P<0.0001$; all draining and fertilizer treatments combined). In the course of the vegetation period, the difference was reduced but not completely eliminated. Final shoot height was in burned plots still an almost significant 8.6% lower than in unburned ones (133.8 vs. 146.4 cm; $P<0.06$) (Fig. 14). There was no significant burning x draining interaction but burning affected shoot height more markedly in the drained basin were the fire had been more severe (Figs. 15 and 16).

On June 19, that is one week after fertilizers had been applied, the Typha plants had not yet responded to the treatments (Fig. 14). Later on, however, differences became apparent and final shoot height differed significantly among the fertilizer treatments ($P<0.0001$) (Figs. 14, 15 and 16). Global evaluation of the data (final heights) with no regard to draining and burning regimes showed shoots to be tallest in NPL- and N-fertilized plots with 161.1 and 148.6 cm, respectively, followed by the P-, L- and unfertilized treatments with 134.0, 129.8 and 126.9 cm, respectively (Appendix 7). The difference between unfertilized and NPL- and N-treatments, respectively, proved to be highly significant ($P<0.0001$). Combining N-, P-, L- and NPL-treatments, the sole distinction being made between fertilized and unfertilized plots, fertilizer effects were more pronounced in drained (136.9 cm in fertilized vs. 118.5 cm in unfertilized plots; contrast C vs. NPL, N, P, L: $P<0.057$) than in undrained (149.9 vs. 135.3 cm; contrast n.s.) treatments and more important under burned (137.4 vs. 119.0 cm; contrast $P<0.04$) than under unburned 149.4 vs. 134.8; contrast n.s.) conditions (Figs. 15 and 16).

Fig. 15 (page 34). Development of mean total shoot height (solid lines) and mean height of the green shoot portion (broken lines) for *Typha glauca* on unburned (left) and burned (right) plots of the undrained basin, on which were superimposed five fertilizer treatments (C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added).

Values are means n = 5. Two draining treatment means (all burning and fertilizer treatments combined, n = 50), two burning treatment means within a single draining regime (all fertilizer treatments combined, n = 25), and two fertilizer treatment means within a single draining x burning regime (n = 5) sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons). In the parentheses following the draining and burning treatment indications, the first letter refers to the mean total shoot height on June 19, the second to the final shoot height (October 3).

Fig. 16 (page 35). Development of mean total shoot height (solid lines) and mean height of the green shoot portion (broken lines) for *Typha glauca* on unburned (left) and burned (right) plots of the drained basin, on which were superimposed five fertilizer treatments (C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added). (For explanations see Fig. 15).


Undrained (a,a) unburned (a,a)
Undrained (a,a) burned (b,a)
Mean shoot height (cm)
0
50
100
150
M
J
J
A
S
O
N
NPL
P
C
L
(a,a)
NPL (a,b)
N
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C
(a,a)

Fig. 15.

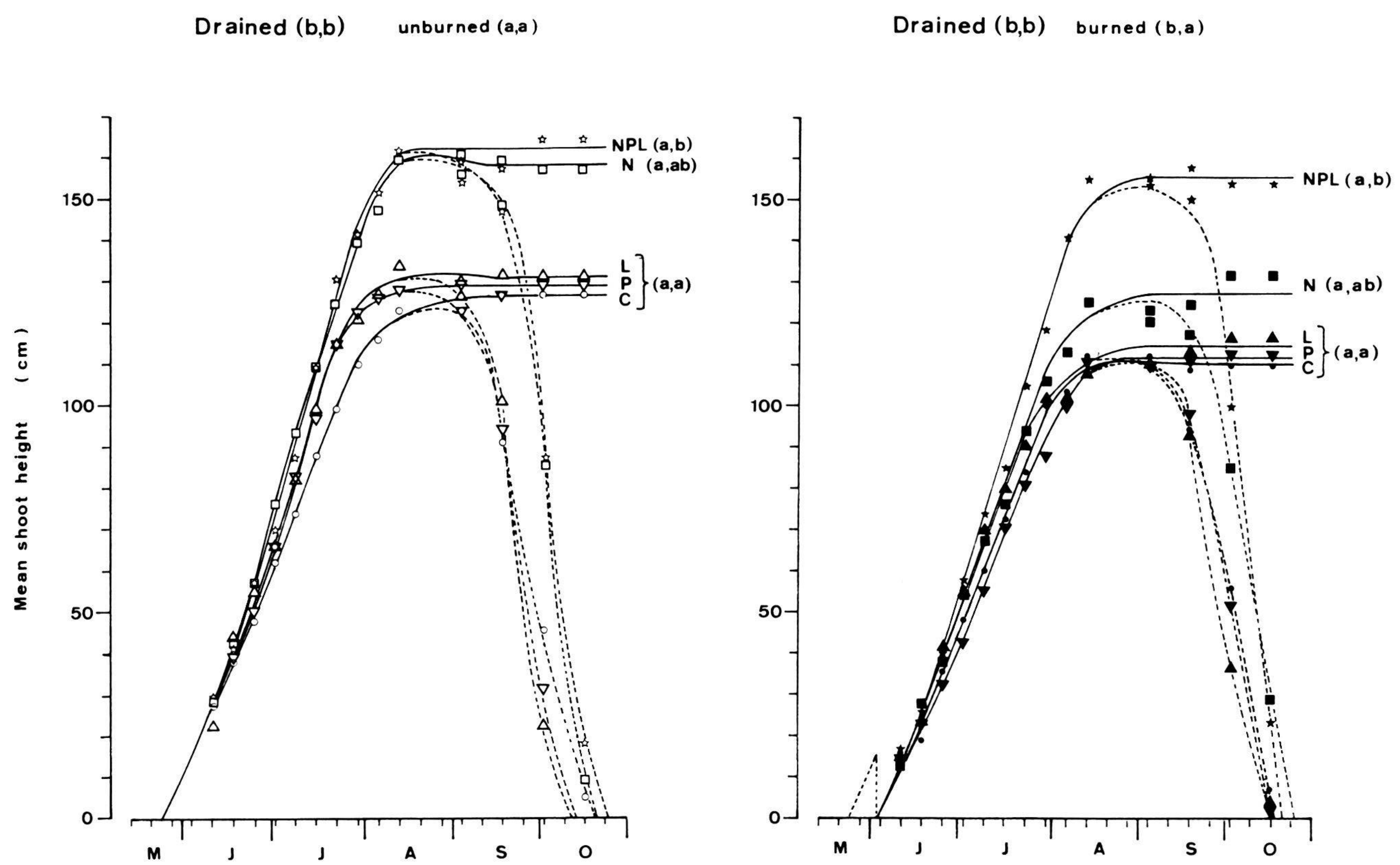

Drained (b,b) unburned (a,a)
Drained (b,b) burned (b,a)
Mean shoot height (cm)
150
100
50
0
M
J
J
A
S
O
NPL (a,b)
N (a,ab)
L
P
C
(a,a)

Fig. 16.

In addition to the quantitative differences in fertilizer effects between the different draining and burning regimes, there were also qualitative differences (Figs. 15 and 16). In the unburned treatments, Typha shoot height was practically the same in both NPL- and N-fertilized plots, whereas in the burned treatments shoot height in N-plots was significantly lower than in NPL-plots ($P<0.02$). Addition of phosphorus increased Typha shoot height considerably, though not significantly, in undrained plots (148.2 vs. 135.3 cm in unfertilized treatments) but did not affect it in drained plots (119.9 vs. 118.5 cm). Liming, on the other hand, resulted in somewhat greater shoot height under drained (124.2 vs. 118.5 cm in unfertilized plots) as well as under burned (125.0 vs. 119 cm) conditions, but had no effect neither in undrained (135.4 vs. 135.3 cm) nor in unburned (134.7 vs. 134.8 cm) treatments.

4.4. BASAL SHOOT CIRCUMFERENCE

The response of basal shoot circumference to the different draining, burning and fertilizer treatments was very similar to that of final shoot height (Figs. 17 and 18, Appendix 8, Table 3). Basal shoot circumference was significantly reduced by draining (60.3 vs. 65.6 mm in undrained plots; $P<0.04$; all burning and fertilizer treatments combined), and somewhat, though not significantly, by burning (61.0 vs. 64.9 mm in unburned plots; n.s.; all draining and fertilizer treatments combined). Global evaluation of the data with no regard to draining and burning treatments showed significant differences among fertilizer treatments ($P<0.0001$). Basal shoot circumference in NPL- and N-treatments was with 77.9 and 73.3 mm, respectively, significantly greater than in unfertilized plots with 54.6 mm ($P<0.0001$). P- and L- treatments, on the other hand, were with 55.9 and 52.4 mm, respectively, not markedly different from unfertilized control plots (Fig. 17).
As was true for final shoot height, basal shoot circumference was significantly higher in NPL- than in N-treatments under burned (79.2 vs. 66.7 mm, $P<0.05$) but not under unburned conditions (76.7 vs. 80.8 mm; n.s.). Addition of phosphorus tended to increase basal shoot circumference in the undrained basin (63.3 vs. 56.1 mm in unfertilized plots; both burn-

ing treatments combined; n.s.) but tended to decrease it in the drained one (48.4 vs. 53.2 mm; n.s.), the difference between the two basins being significant (63.3 vs. 48.5 mm, P<0.02). Liming did not affect basal shoot circumference in the undrained treatments (55.9 vs. 56.1 mm in unfertilized plots; n.s.; both burning treatments combined) but decreased it somewhat in the drained ones (49.0 vs. 53.2 mm; n.s.).

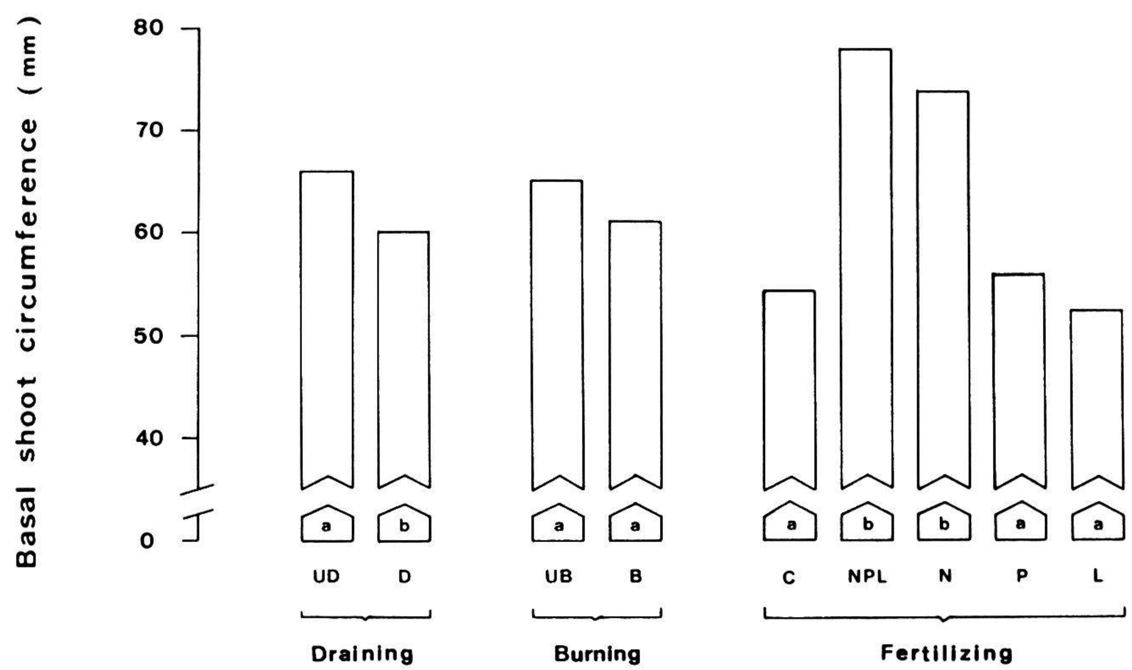


Fig. 17. Basal shoot circumference of Typha glauca under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at P<0.05 (unplanned pairwise comparisons).

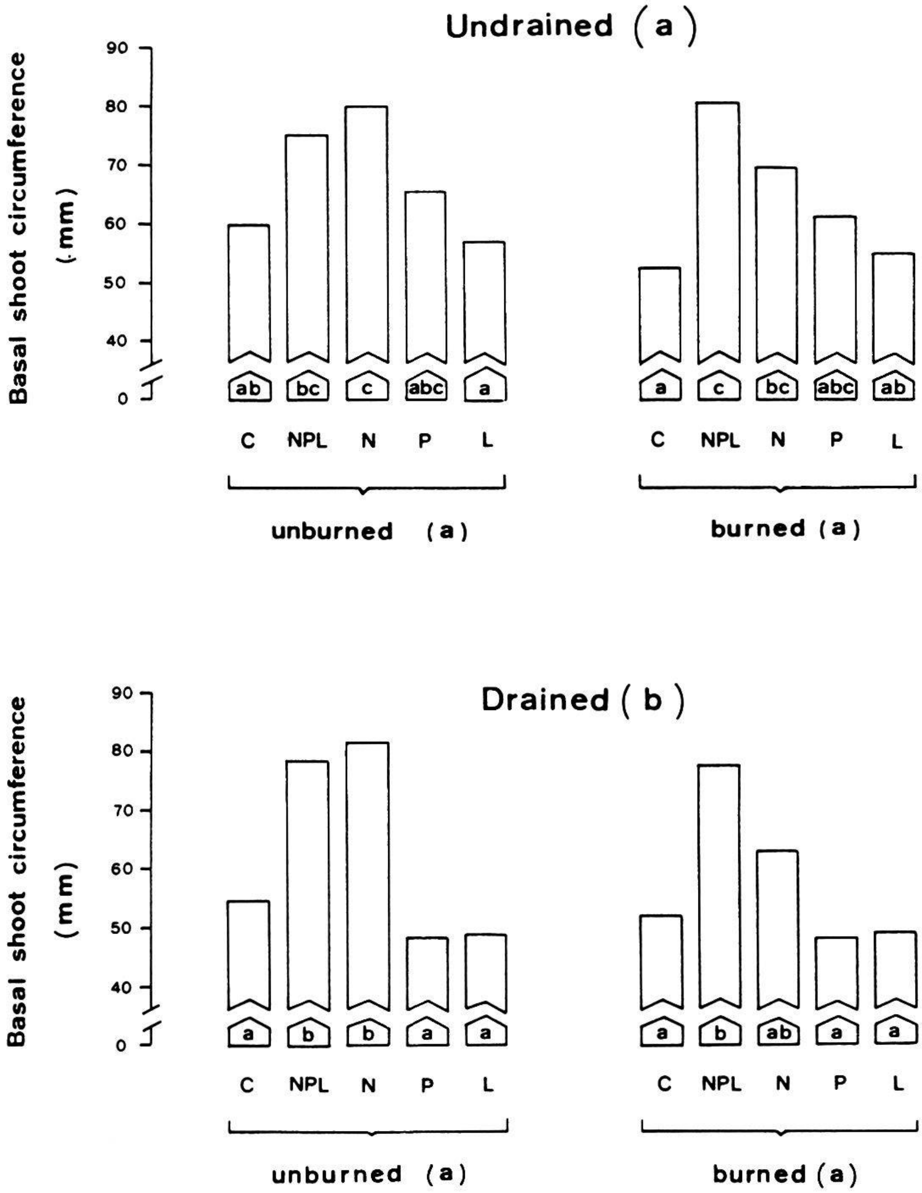


Fig. 18. Basal shoot circumference of <u>Typha glauca</u> in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 5. Two draining means (all burning and fertilizer treatments combined; n = 50), two burning means within a single draining regime (all fertilizer treatments combined, n = 25) and two fertilizer means within a single draining x burning regime (n = 5) sharing the same letter are not significantly different at P<0.05 (unplanned pairwise comparisons).

4.5. NUMBER OF LEAVES PER SHOOT

Draining, burning and fertilizing affected the number of leaves per shoot in much the same way as final shoot height and basal shoot circumference (Figs. 19 and 20, Appendix 9, Table 3). Draining as well as burning reduced the number of leaves, but in both cases the reduction was not significant. Differences among the fertilizer treatments, on the other hand, were again highly significant ($P<0.0001$; all draining and burning treatments combined).

Global evaluation of the data with no regard to draining and burning treatments showed the number of leaves to be highest in NPL- and N-treatments with 9.63 and 9.02 leaves per shoot, respectively, followed by P-, C- and L-treatment plots with 7.97, 7.74 and 7.60 leaves per

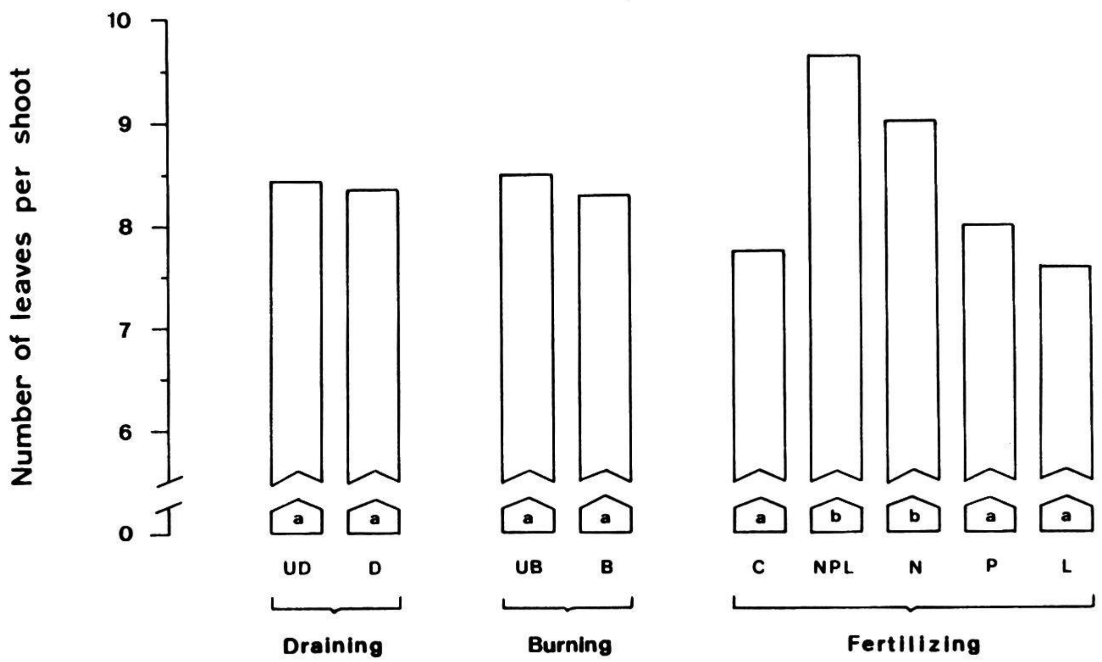


Fig. 19. Number of leaves per shoot of <u>Typha glauca</u> under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons).

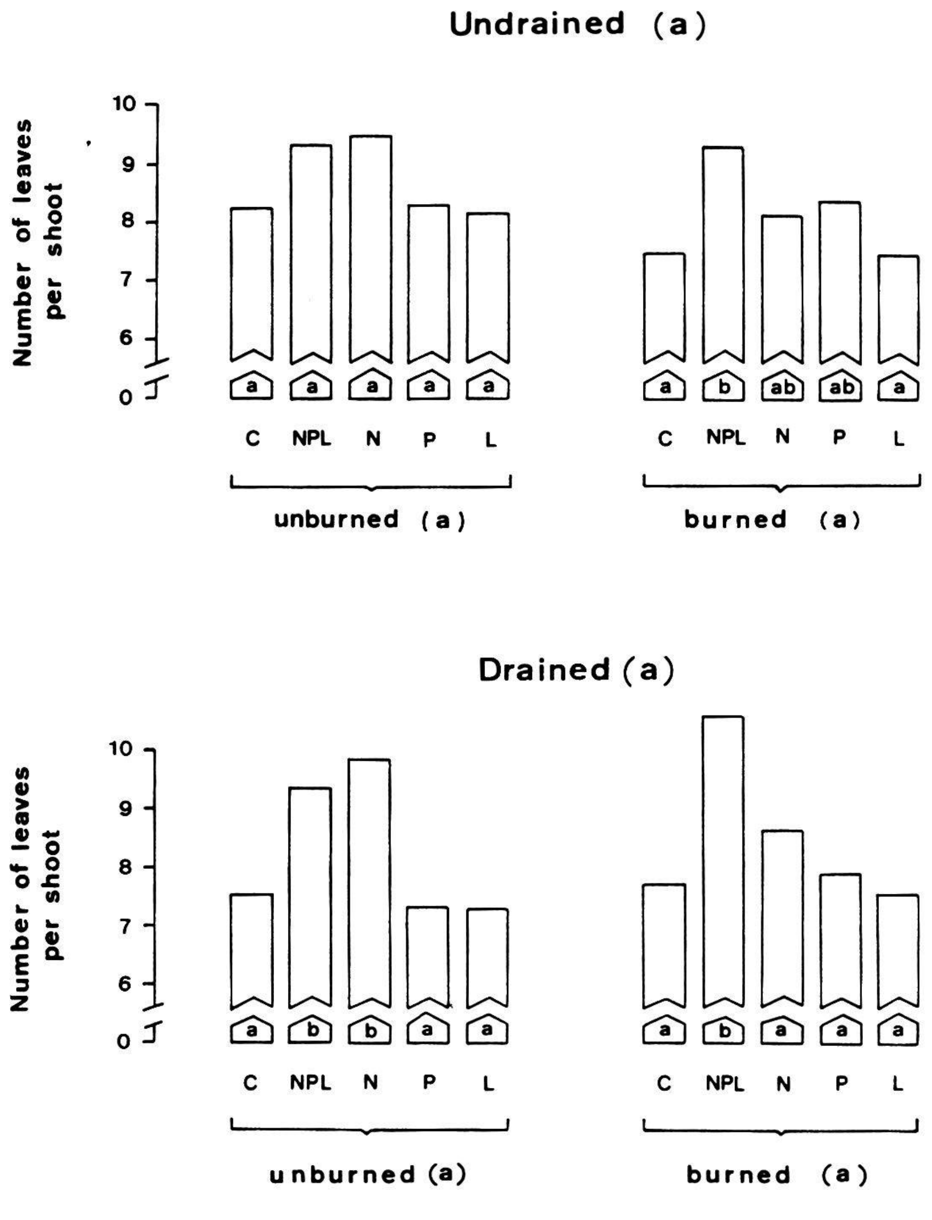


Fig. 20. Number of leaves per shoot of Typha glauca in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 5. Two draining means (all burning and fertilizer treatments combined; n = 50), two burning means within a single draining regime (all fertilizer treatments combined, n = 25) and two fertilizer means within a single draining x burning regime (n = 5) sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons).

shoot (Appendix 9). The difference between unfertilized and NPL- and N-fertilized plots, respectively, was again highly significant ($P<0.0001$). Combining NPL-, N- P- and L-treatments, the sole distinction being made between fertilized and unfertilized plots, fertilizer impact was the same for the two draining as well as for the two burning regimes.
The response to a given fertilizer treatment, however, was again not always the same in the different draining and burning regimes, the burning x fertilizer interaction being significant ($P<0.02$) and the draining x fertilizer interaction almost significant ($P<0.06$) (Table 3, Fig. 20). Addition of nitrogen in combination with phosphorus and lime increased the number of leaves per shoot significantly more than did application of nitrogen alone under burned (9.93 vs. 8.39 leaves per shoot; $P<0.001$) but not under unburned conditions where the difference between NPL- and N-treatments was not significant (9.33 vs. 9.66 leaves per shoot; n.s.). Fertilizing with phosphorus tended to increase the number of leaves under undrained-burned conditions (8.37 vs. 7.44; n.s.) but did not affect it at all under the other draining x burning regimes (Fig. 20). Liming did not change the number of leaves per shoot in the undrained basin (7.80 vs. 7.84 in unfertilized plots; both burning treatments combined) but reduced it somewhat in the drained one (7.40 vs. 7.63; n.s.).

4.6. ASSIMILATION PERIOD

The different draining, burning and fertilizer treatments affected directly the length of the assimilation period. Length of assimilation period was quantified in two ways. First, as the period of time in days between the date when the first shoot emerged in spring and the date when the last shoot became entirely brown in autumn (assimilation period 0%, short AP 0% (Fig. 7). Second, as the period in days between the date when in spring shoot height reached 50% of the final height and the date when in autumn the height of the green shoot portion fell below the 50% mark (assimilation period 50%, short AP 50%). The assimilation period 50% represents the period of time during which the main bulk of photosynthesis is accomplished.
Draining reduced the length of the assimilation period considerably. In

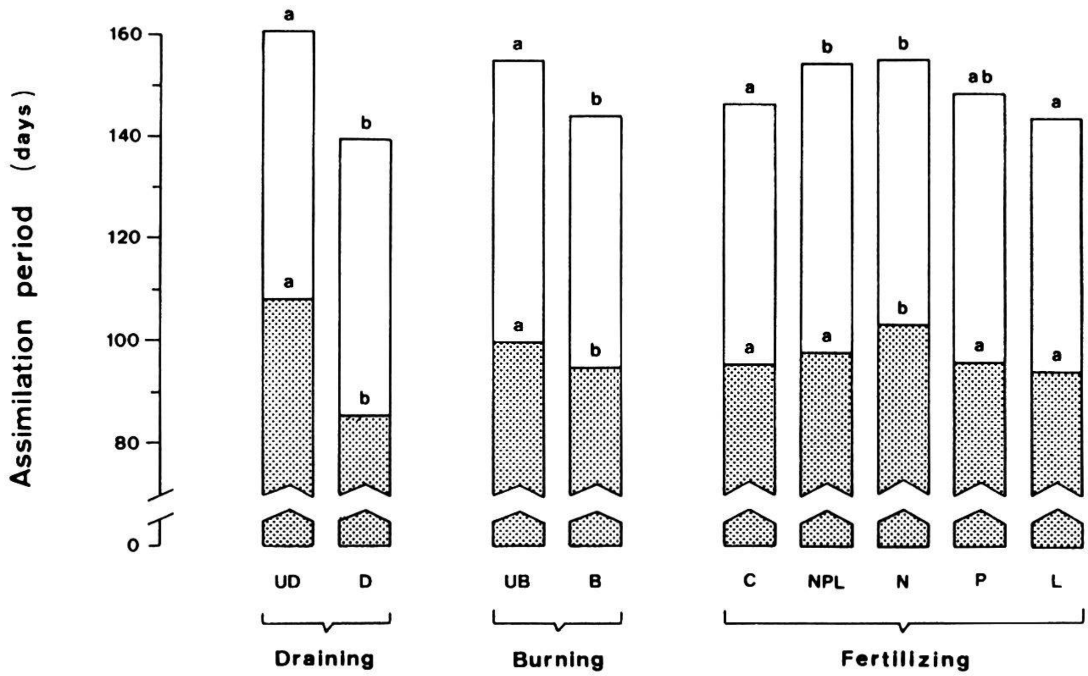
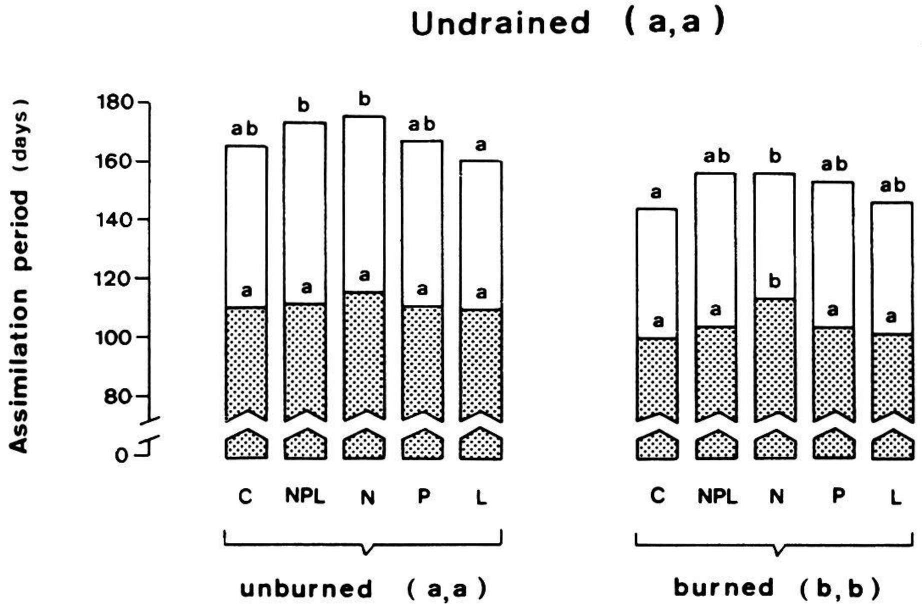


Fig. 21. Length of the assimilation periods 50% (AP 50%, shaded portion) and 0% (AP 0%, entire bars) of Typha glauca under different draining, burning and fertilizer treatments. **Draining treatments:** UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons). For definitions of AP 0% and AP 50% see Fig. 7.

the drained basin, the assimilation periods 0% and 50% were on average 21.5 days ($P<0.0001$; all burning and fertilizer treatments combined) and 22.3 days ($P<0.0001$) shorter than in the undrained basin, that is 13.4% and 20.6%, respectively (Fig. 21, Appendices 10 and 11). Delayed start of growth in spring accounted for 31.6% and 43.9%, respectively, of the difference in AP 0% and AP 50% between the two draining treatments. In the drained basin, the first shoots emerged 6.8 days later than in the undrained basin ($P<0.0001$; all burning and fertilizer treatments combined), and they reached 50% of their final height 9.8 days later ($P<0.0001$) (Fig. 23, Appendices 12 and 13). The remaining 68.4% and 56.1% of the difference, respectively, were due to a more rapid rate of senescence under drained than under undrained conditions as illustrated below (Fig. 27).



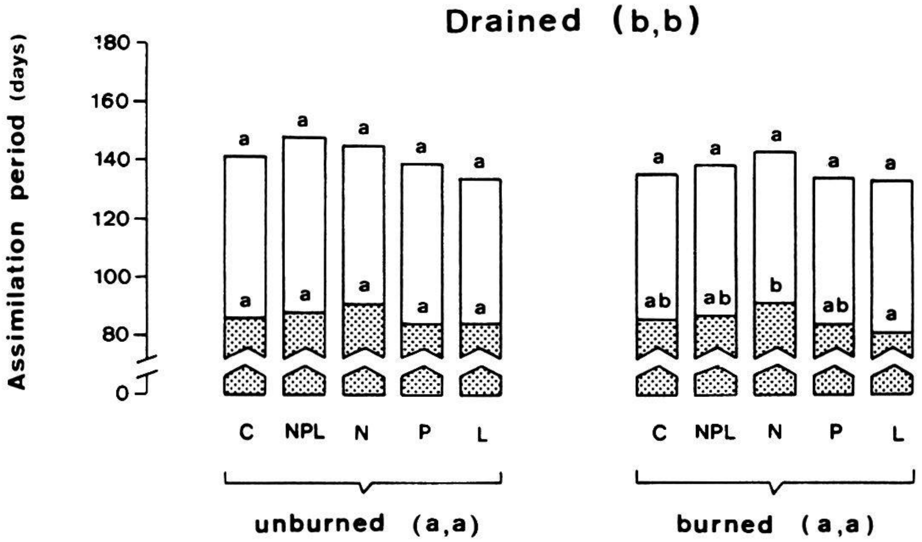


Fig. 22. Length of the assimilation periods 50% (AP 50%, shaded portion) and 0% (AP 0%, entire bars) of Typha glauca in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Values are means n = 5. Two draining treatment means (all burning and fertilizer treatments combined; n = 50), two burning means within a single draining regime (all fertilizer treatments combined, n = 25) and two fertilizer treatment means within a single draining x burning regime (n = 5) sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons). In the parentheses following draining and burning treatment indications, the first letter refers to AP 50% (shaded) and the second to AP 0% (entire bars). For definitions of AP 0% and AP 50% see Fig. 7.

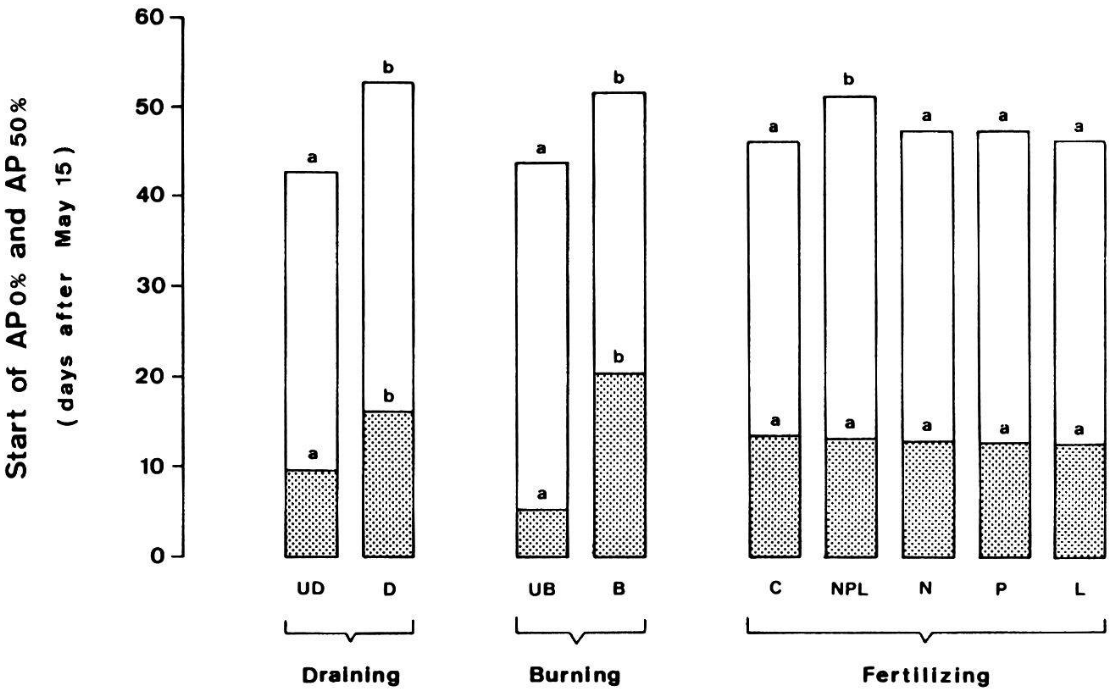


Fig. 23. Start of the assimilation periods 50% (AP 50%, shaded portion) and 0% (AP 0%, entire bars) of Typha glauca under different draining, burning and fertilizer treatments. **Draining treatments:** UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at P<0.05 (unplanned pairwise comparisons). For definitions of AP 0% and AP 50% see Fig. 7.

Burning resulted likewise in a significantly reduced assimilation period (Fig. 21). Draining and fertilizer treatments combined, the difference between burned and unburned treatments amounted for the assimilation periods 0% and 50% to 10.9 days (P<0.0002) and 4.0 days (P<0.005), that is by 7.0% and 4.0%, respectively (Appendices 10 and 11). However, the extent to which burning reduced the length of the assimilation period depended considerably upon the draining regime, the draining x burning interaction being significant for both AP 0% (P<0.006) and AP 50% (P<0.02) (Table 3, Fig. 22). Under undrained conditions, the assimilation periods 0% and 50% were in burned plots 17.0 days (P<0.0005) and 7.0 days (P<0.02), that is 10.1% and 6.3%, respectively, shorter than in the unburned treatment plots. In contrast, under drained conditions the reductions were with 4.9 and 1.0 days, that is 3.6% and 1.2%, respectively, much smaller and not significant (Appendices 10 and 11).

Whereas late shoot emergence in drained plots accounted for less than half of the difference between the two draining treatments, delayed start of spring growth in burned as compared to unburned plots accounted for the entire difference in the length of the assimilation periods between the two burning treatments. In fact, the differences between the dates on which the assimilation periods 0% and 50% started in the two burning treatments were larger by 3.9 and 3.6 days, that is 36% and 90%, respectively, than between the length of the respective assimilation periods (Figs. 21 and 23, Appendices 10-13). The late start in spring was, therefore, to some extent compensated for by a slower rate of senescence in autumn (see below and Fig. 27). In burned plots, the first shoots emerged 14.8 days later than in unburned treatment plots ($P<0.0001$; all draining and fertilizer treatments combined), and they reached 50% of their final height 7.6 days later ($P<0.0001$) (Fig. 23, Appendices 12 and 13).

As was true for the length of the assimilation period, the delay in the start of the assimilation period brought about by burning was much more pronounced under undrained than under drained conditions (Fig. 24); the draining x burning interaction was, however, only significant as regards the beginning of the assimilation period 0% ($P<0.003$) but not as regards the start of the assimilation period 50% (Table 3). In the burned plots of the undrained basin, the assimilation periods 0% and 50% started 19.0 and 9.0 days later than in the unburned treatment plots ($P<0.0001$ and $P<0.008$; all fertilizer treatments combined), whereas the respective delays in the drained basin amounted to only 10.5 and 6.0 days ($P<0.007$ and $P<0.003$) (Appendices 12 and 13). However, spring growth commenced later in burned as compared to unburned plots only in the year in which the burning was carried out, the fire consuming all the shoots that had already emerged at the time of burning. In the year following fire, in contrast, spring growth started earlier in burned than in unburned plots, due to more favourable microclimatic conditions in the former ones (KRüSI and WEIN 1988).

Global evaluation of the data with no regard to draining and burning regimes showed significant differences among the fertilizer treatments for both assimilation periods considered ($P<0.0001$) (Fig. 21, Table 3). Fertilizing with nitrogen alone (N-plots) or in combination with phosphorus

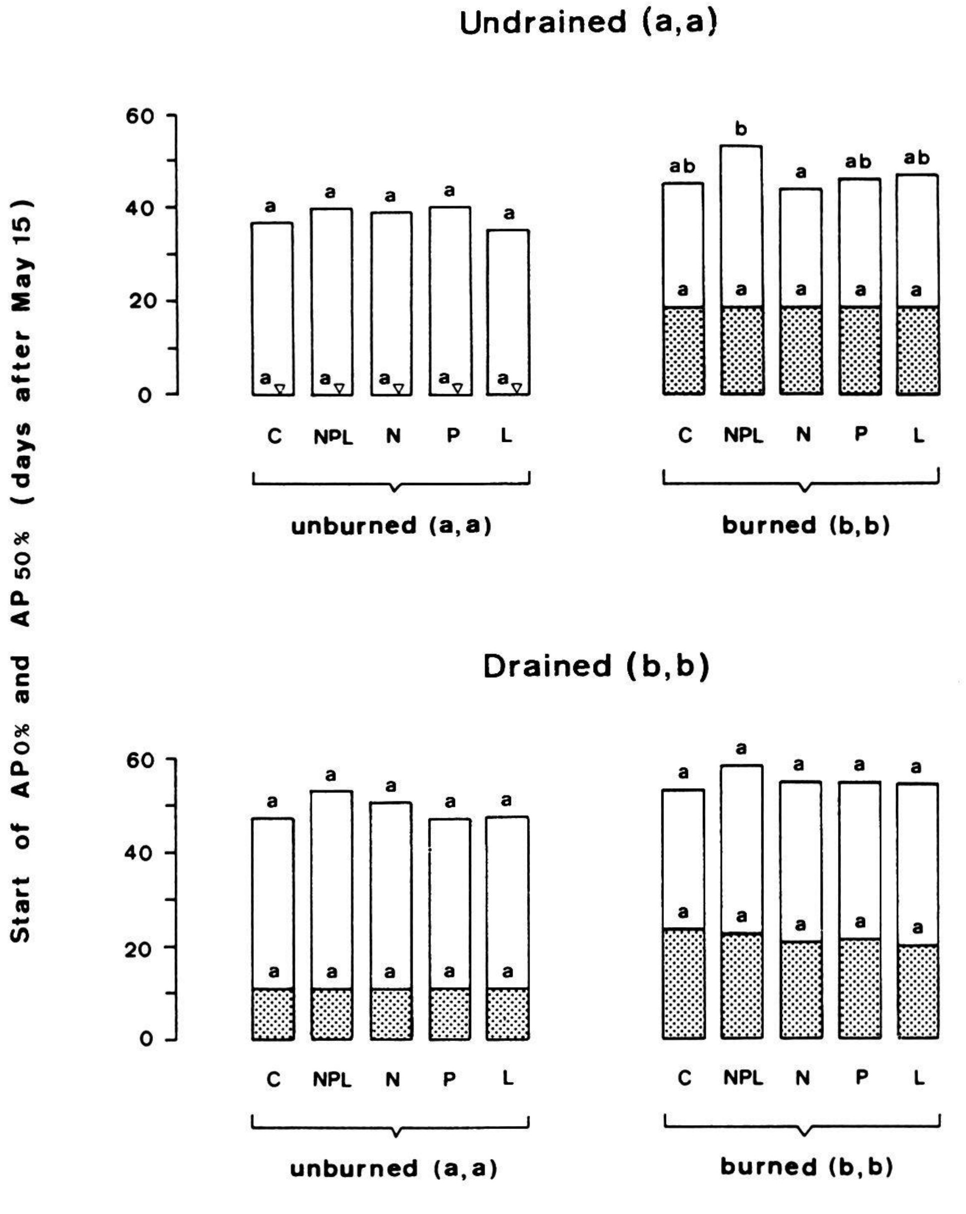


Fig. 24. Start of the assimilation periods 50% (AP 50%, shaded portion) and 0% (AP 0%, entire bars) of Typha glauca in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Values are means n = 5. Two draining treatment means (all burning and ferilizer treatments combined, n = 50), two burning treatment means within a single draining regime (all fertilizer treatments combined, n = 25) and two fertilizer treatments means within a single draining x burning regime (n = 5) sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons). In the parentheses following the draining and burning treatment indications, the first letter refers to the start of AP 50% (shaded portion) and the second to the beginning of AP 0% (entire bars). For definitions of AP 0% and AP 50% see Fig. 7.

and lime (NPL-plots extended the assimilation period. In N-fertilized plots, both AP 0% and AP 50% were a significant 8.6 and 7.5 days, that is 5.9% and 7.8%, respectively, longer than in unfertilized C-plots ($P<0.001$ and $P<0.0001$; all draining and burning treatments combined); in NPL-fertilized plots, the respective prolongations were 7.6 and 2.1 days, that is 5.2% and 2.2%, only the one of AP 0% being significant ($P<0.004$) (Appendices 10 and 11, Table 3). In contrast, addition of phosphorus did practically not change the duration of the two periods considered, prolonging AP 0% by 2.2 days (1.5%) and AP 50% by 0.2 days (0.2%), and liming shortened the two periods by not significant 2.7 days (1.8%) and 1.2 days (1.3%), respectively (Fig. 21, Appendices 10 and 11). Fertilizer effects were very similar in the two draining as well as in the two burning treatments, neither the fertilizer x draining nor the fertilizer x burning interaction being significant (Fig. 22, Table 3).
Since fertilizer were applied only after the first shoots had emerged in most of the permanently marked quadrats, fertilizing did not affect the beginning of the assimilation period 0%; the commencement of the assimilation period 50%, on the other hand, differed significantly among the fertilizer treatments ($P<0.002$; all draining and burning treatments combined) (Fig. 23, Table 3, Appendices 12 and 13). Global evaluation of the data with no regard to draining and burning treatments showed that *Typha* plants reached 50% of their final height significant 5.0 days later in NPL-fertilized as compared to unfertilized C-plots ($P<0.0001$), and not significant 1.0, 1.0 and 0 days later in N-, P- and L-treatment plots, respectively. The relative to unfertilized plots longer assimilation periods observed in the N- and NPL-fertilized plots were, therefore, entirely due to a delayed senescence in the fall (see below, Fig. 27), and the prolongation brought about by the treatments would have been even more pronounced as regards the assimilation period 50% had it not been for the late start in spring in the N- and particularly in the NPL-treatment plots.
The fact that the *Typha* plants in the NPL-plots reached 50% of their final height later than the *Typha* plants in the unfertilized plots does, however, not mean that they grew less rapidly in the NPL- than in the unfertilized C-plots. On the contrary, the *Typha* plants gained height more rapidly in plots fertilized with nitrogen alone (N-plots) or in combination with phosphorus and lime (NPL-plots) than in unfertilized C-treatment plots (Figs. 15 and 16). This became clear when for all fer-

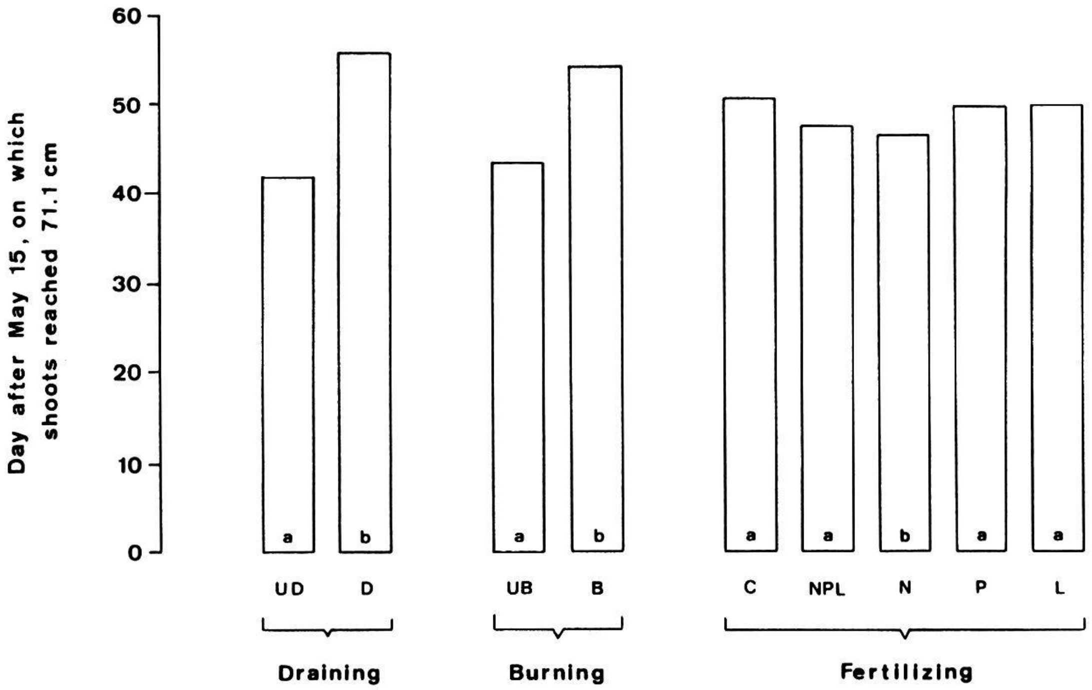


Fig. 25. Day after May 15, on which mean shoot height of Typha glauca reached 71.1 cm, that is 50% of the final height in the undrained, unburned and unfertilized treatment plots, under different draining, burning and fertilizer treatments. **Draining treatments:** UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons).

tilizer treatments the dates were compared on which Typha plants had reached a given common height of reference instead of 50% of their final height, which differed, of course, among the treatments (Figs. 25 and 26). If, for instance, 50% of the final shoot height in the undrained, unburned and unfertilized treatments, that is 71.1 cm, was used as reference height, global evaluation of the data with no regard to draining and burning treatments showed that Typha plants reached that height first in N- and NPL-plots, followed by P-, L- and C-treatment plots (Fig. 25). In N- and NPL-plots, the reference height of 71.1 cm was reached significant 4.1 days and almost significant 3.1 days, respectively, earlier than in unfertilized C-plots ($P<0.01$ and $P<0.059$; all draining and burning treatments combined); the advance of 0.6 and 0.4

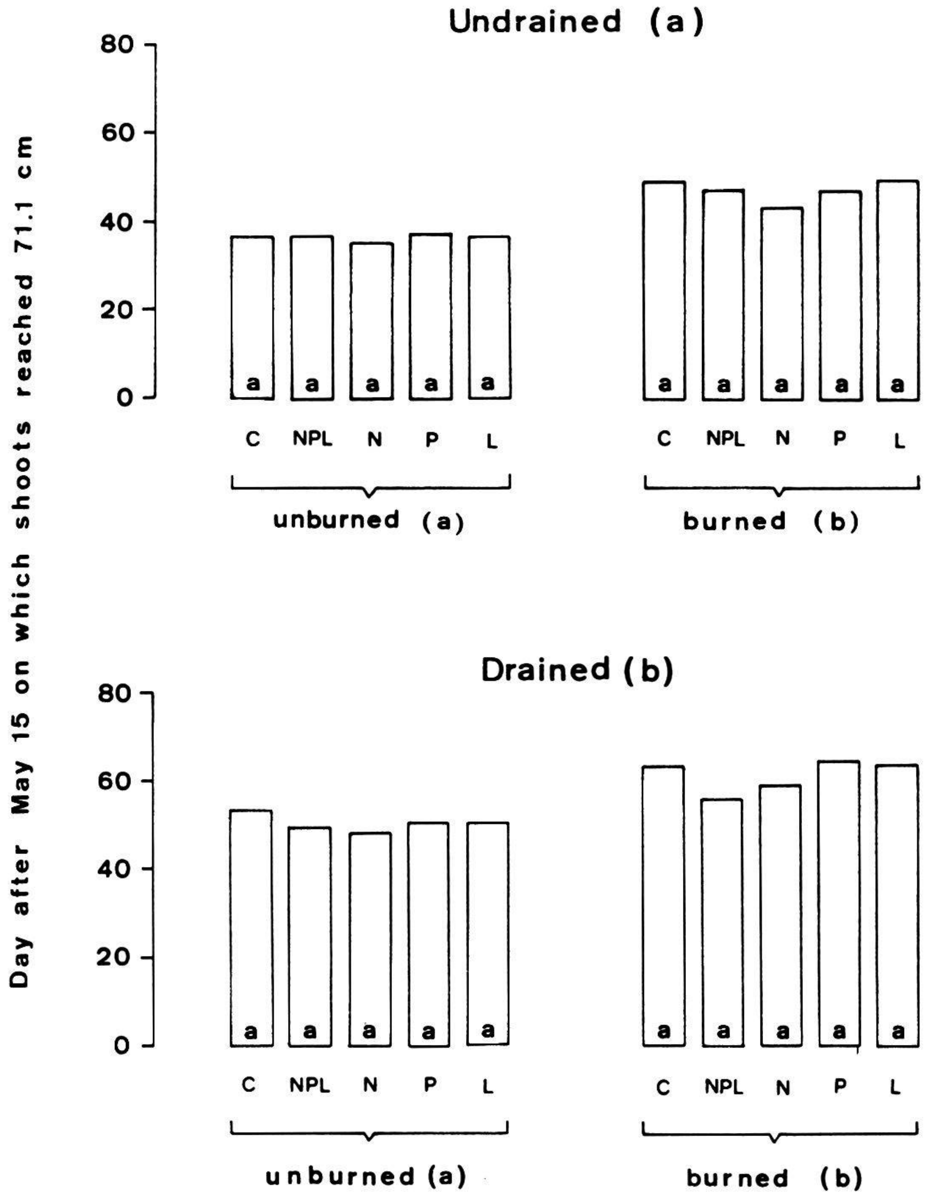


Fig. 26. Day after May 15, on which mean shoot height of <u>Typha glauca</u> reached 71.1 cm, that is 50% of the final height in the undrained, unburned and unfertilized treatment plots, in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 5. Two draining means (all burning and fertilizer treatments combined; n = 50), two burning means within a single draining regime (all fertilizer treatments combined, n = 25) and two fertilizer means within a single draining x burning regime (n = 5) sharing the same letter are not significantly different at P<0.05 (unplanned pairwise comparisons).

days in the P- and L-treatment plots was, on the other hand, not significant (Appendix 14, Table 3). Fertilizer impact was slightly more pronounced in the drained than in the undrained basin and somewhat more important in burned as compared to unburned plots (Fig. 26), but neither the fertilizing x draining nor the fertilizing x burning interactions were significant (Table 3).

4.7. SENESCENCE

The onset of senescence was not affected by the different draining, burning and fertilizer treatments (Figs. 15 and 16). Under all treatment combinations, it commenced by mid-August. In contrast, the rate of the senescence process and, in consequence, the date on which it was complete differed significantly among the treatments (Figs. 27 and 28, Table 3).

The rate of senescence was expressed in two ways. First, as the day after the onset of senescence, i.e.August 14, on which the senescence process was halfway through, that is the day on which the mean height of the green portion of the shoots fell below 50% of the mean total shoot height (Appendix 15). Second, the day after August 14 on which the senescence process was to 100% complete, that is when all the shoots had become entirely brown (Appendix 16). In addition, the mean height of the green portion of the shoots in percent of the mean total shoot height is shown for October 3, in order to give an impression of the actual situation in the field on a given day (Appendix 17).

Draining accelerated the process of senescence considerably. In the drained treatments, senescence was complete to 50 and 100%, respectively, 12.5 and 14.7 days earlier than in the undrained treatments ($P<0.0001$; all burning and fertilizer treatments combined) (Fig. 27, Appendices 15 and 17). And on October 3, only the lower 44.0% of the shoots were still green in the drained as compared to 72.6% in the undrained basin ($P<0.0001$; all burning and fertilizer treatments combined) (Fig. 29, Appendix 17).

Burning, on the other hand, slowed the rate of senescence down. In the burned treatments, the green height fell below 50% of the total shoot

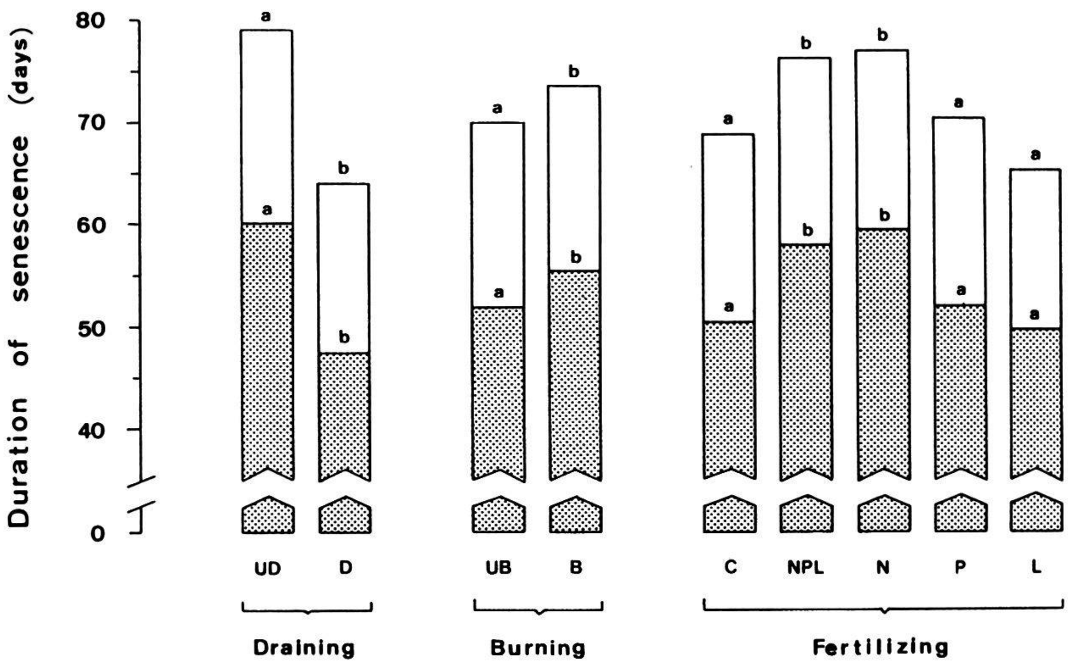
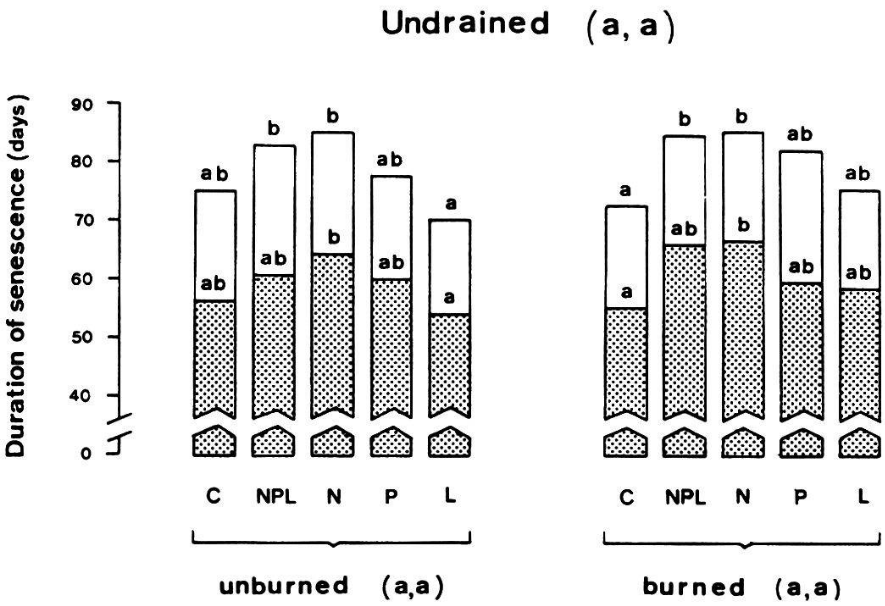


Fig. 27. Duration of senescence 50% (DS 50%, shaded portion) and 100% (DS 100%, entire bars) of Typha glauca under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at P<0.05 (unplanned pairwise comparisons). For definitions of DS 50% and DS 100% see Fig. 7).

height 3.5 days later as compared to unburned treatments (P<0.007; all draining and fertilizer treatments combined) and the senescence process was complete 3.8 days later (P<0.03) (Fig. 27). And on October 3, the lower 63.2% of the shoots in burned plots were still green as opposed to 53.4% in unburned plots (P<0.03; all draining and fertilizer treatments combined) (Fig. 29). There was no significant draining x burning interaction but burning affected the rate of senescence more markedly in the drained basin (Table 3, Fig. 28, Appendices 15-17). In the drained basin, senescence was halfway through 5.2 days later in burned than in unburned plots (P<0.03; all fertilizer treatments combined) and it was complete 5.6 days later (P<0.06). The respective differences in the undrained basin. on the other hand, were with only 2.0 and 2.0 days,



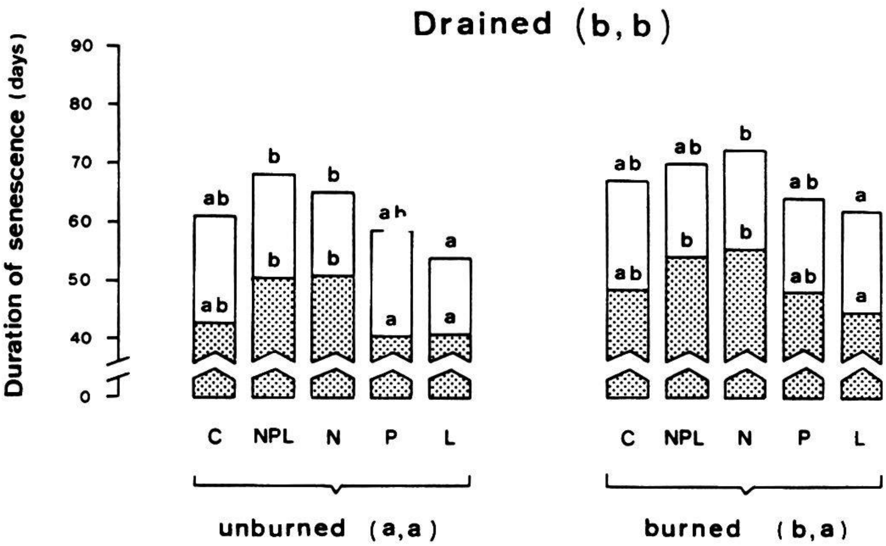


Fig. 28. Duration of senescence 50% (DS 50%, shaded portion) and 100% (DS 100%, entire bars) of Typha glauca, in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Values are means n = 5. Two draining treatment means (all burning and fertilizer treatments combined, n = 50), two burning treatment means within a single draining regime (all fertilizer treatments combined, n = 25) and two fertilizer treatment means within a single draining x burning regime (n = 5) sharing the same letter are not significantly different at P<0.05 (unplanned pairwise comparisons). In the parentheses following the draining and burning treatment indications, the first letter refers to SD 50% (shaded portion) and the second to SD 100% (entire bars). For definitions of DS 50% and DS 100% see Fig. 7.

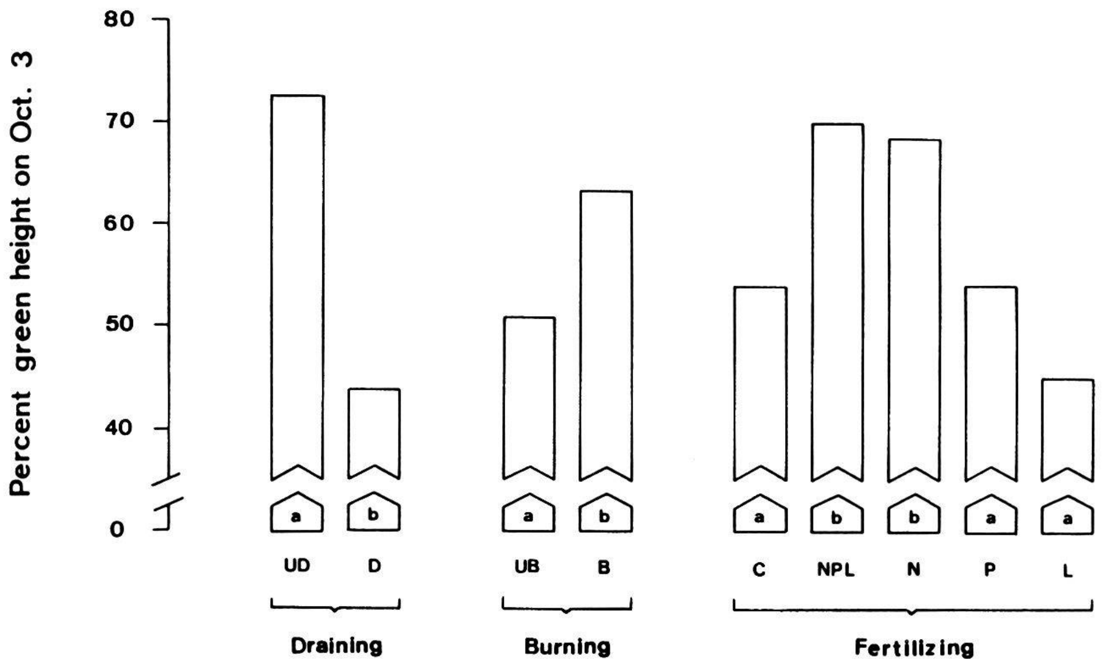


Fig. 29. Height of the green shoot portion of Typha glauca on October 3, in percent of total shoot height, under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons).

respectively, much less distinct (both n.s.). And on October 3, green height amounted in the burned and unburned plots of the drained basin to 52.3 and 35.6%, respectively, of the total shoot height (all fertilizer treatments combined; difference n.s.) as compared to 74.0 and 71.1%, respectively, in the undrained basin (n.s.)(Fig. 30, Appendix 17).
Global evaluation of the data with no regard to draining and burning regimes showed significant differences among fertilizer treatments ($P<0.0001$) for all three parameters considered (Table 3, Figs. 27 and 29). Fertilizing with nitrogen alone (N-plots) or in combination with phosphorus and lime (NPL-plots) slowed the senescence process significantly down. In N- and NPL-fertilized plots senescence had reached the half-point 8.6 and 7.2 days, respectively, later than in unfertilized

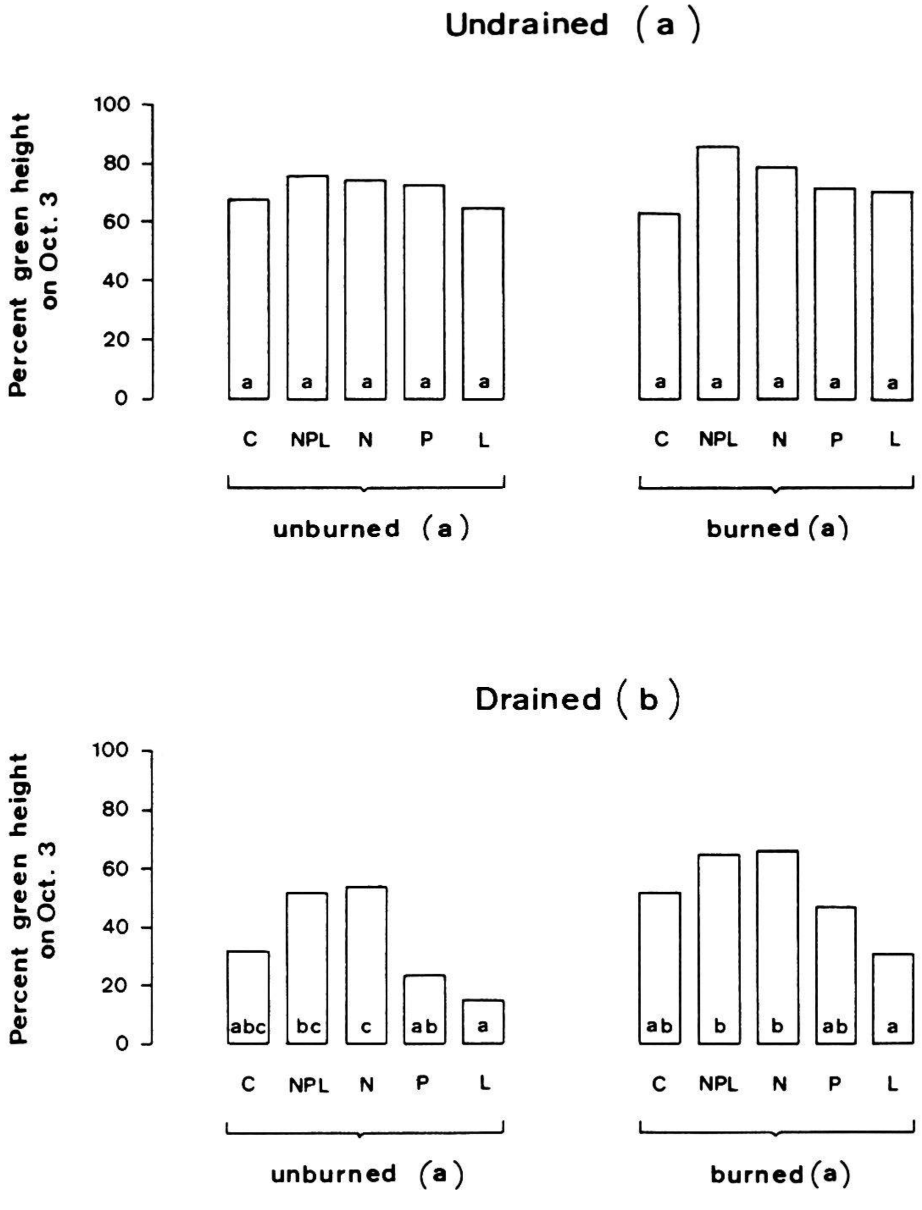


Fig. 30. Height of the green shoot portion of <u>Typha glauca</u> on October 3, in percent of total shoot height, in response to different fertilizer treatments which were superimposed on four draining x burning regimes.

Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 5. Two draining means (all burning and fertilizer treatments combined; n = 50), two burning means within a single draining regime (all fertilizer treatments combined, n = 25) and two fertilizer means within a single draining x burning regime (n = 5) sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons).

plots ($P<0.0001$ and $P<0.0003$; all draining and burning treatments combined), and it was complete 7.9 and 7.3 days later, respectively ($P<0.001$) (Fig. 27, Appendices 15 and 16). On October 3, percent green height in N- and NPL-fertilized plots was with 68.4 and 69.7%, respectively, significantly greater relative to 53.9% in unfertilized C-plots ($P<0.003$ and $P<0.001$, respectively) (Fig. 29, Appendix 17). Addition of phosphorus, on the other hand, reduced the rate of senescence only slightly, and liming accelerated the process to some extent (Figs. 27 and 29). In phosphorus fertilized plots, senescence was complete to 50 and 100%, respectively, 1.4 and 1.6 days later than in unfertilized plots, and the percent height of the green shoot portion was with 54.1% practically the same as in the unfertilized treatments (53.9%). In limed plots, the upper 50% of the shoots had become yellow only 1.1 days earlier than in unfertilized plots but they were completely yellow an almost significant period of 3.6 days earlier ($P<0.054$; all draining and burning treatments combined); and on October 3, the green portion of the shoots in limed plots was with 45.2% of the total height distinctly below the 53.9% in the unfertilized treatments (Figs. 27 and 29, Appendices 15-17).

Fertilizer effects were very similar in the two burning regimes but somewhat different in the two draining treatments; the draining x fertilizer interaction approached, however, the 5% significance level only in the case of the percent green height on October 3 ($P<0.052$) (Table 3, Figs. 28 and 30). During the first half of the senescence process, fertilizing with nitrogen alone (N-plots) or in combination with phosphorus and lime (NPL-plots) slowed yellowing down to much the same extent in the two draining treatments; during the second half of senescence, on the other hand, yellowing was slowed down much more distinctly in N- and NPL-fertilized plots under undrained than under drained conditions (Figs. 28 and 30, Appendices 15 and 16). Senescence reached the half-point 9.7 ($P<0.002$) and 7.6 ($P<0.01$) days later in N- and NPL-fertilized plots of the undrained basin than in the respective unfertilized treatments, and 7.4 ($P<0.003$) and 6.8 ($P<0.005$) days later in the drained basin, respectively. By contrast, senescence was complete in N- and NPL-treatment plots of the undrained basin a significant 11.4 ($P<0.001$) and 10.0 ($P<0.002$) days later than in unfertilized C-treatments whereas the respective delays in the drained basin amounted to only 4.3 (n.s.) and 4.5 (n.s.) days, respectively. On the other hand, the difference in percent height of the green shoot portion on October 3 between N- and NPL-fertilized treatment plots on the one hand and unfertilized ones on the other was with 11.4 (n.s.) and 15.4% ($P<0.02$), respectively, smaller in the undrained than in the drained basin where it amounted to 17.6 and 16.3%, respectively (both $P<0.02$) (Fig. 30, Appendix 17). This is due to the fact that, on October 3, senescence was considerably more advanced in the drained than in the undrained treatments (Figs. 15, 16 and 29) and that the rate of yellowing was smaller in the beginning than towards the end of the process.

Addition of phosphorus slowed the process of senescence down in the undrained but tended to accelerate it in the drained basin (Figs. 28 and 30, Appendices 15-17). In the undrained basin, senescence was halfway through 4.0 (n.s.) and complete a significant 6.0 ($P<0.05$) days later in phosphorus fertilized than in unfertilized plots; and the percent height of the green shoot portion on October 3, was somewhat higher too in P-fertilized plots than in unfertilized control treatments (72.5 vs. 65.4%; n.s.). In phosphorus fertilized plots of the drained basin, by contrast, senescence was to 50% and 100% complete 1.4 and 3.0 days, respectively, earlier than in unfertilized treatments (both n.s.), and on October 3, the percent height of the green shoot portion was somewhat lower in P-fertilized relative to unfertilized plots (35.8 vs. 42.4%; n.s.) (Figs. 28 and 30, Appendices 15-17).

Liming did practically not affect the rate of senescence under undrained but accelerated it under drained conditions (Figs. 28 and 30, Appendices 15-17). In the undrained basin, senescence reached the half-point in limed plots 0.6 days later than in the unfertilized ones but was complete 0.9 days earlier; and on October 3, the percent height of the green shoot portion was in limed plots only slightly higher than in the unfertilized ones (67.4 vs. 65.4%). In the drained basin, on the other hand, senescence was halfway through 2.8 (n.s.) and complete a substantial 6.4 ($P<0.02$) days earlier in limed than in unfertilized treatment plots, and the percent height of the green shoot portion was on October 3 with 23.0% significantly smaller than the 42.4% in unfertilized control plots ($P<0.03$).

4.8. SUSCEPTIBILITY TO DROUGHT

Leaf die-back was not only observed during senescence but also during a spell of low rainfall between late May and mid-June, when during a period of 22 days only 5.5 mm of rain were recorded (Fig. 4). Susceptibility to drought was expressed as leaf die-back in percent of total shoot height. For analysis of variance the data of June 19 were used, that is when the die-back was most extreme (Fig. 31, Appendix 18).
As would be expected, percent leaf die-back was much higher in the drained (9.2%; all burning and fertilizer treatments combined) than in the undrained basin (0%), where low rainfall was of little consequence (P<0.0001) (Fig. 32, Appendix 18, Table 3). Likewise percent leaf die-back was much more important in burned than in unburned plots (7.8 vs. 1.4%; all draining and fertilizer treatments combined; P<0.03). As regards the fertilizer treatments, global analysis of the data with no

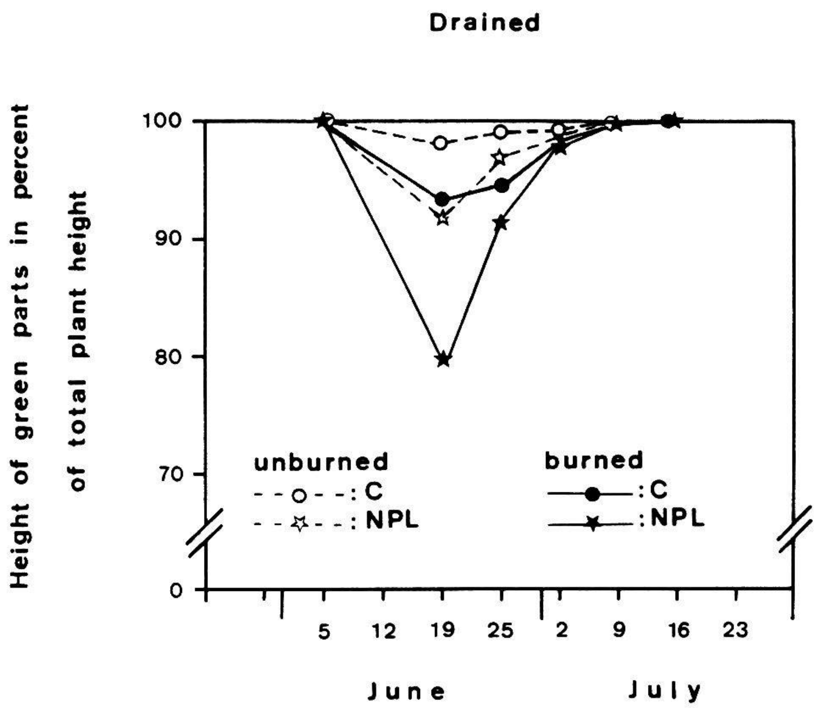


Fig. 31. Susceptibility of Typha glauca to drought: Height of green parts in percent of total plant height, during June and July 1982, in the drained treatment on which were superimposed burning and fertilizer treatments.
C: unfertilized; NPL: nitrogen, phorphorus and lime added. Values are means n = 5.

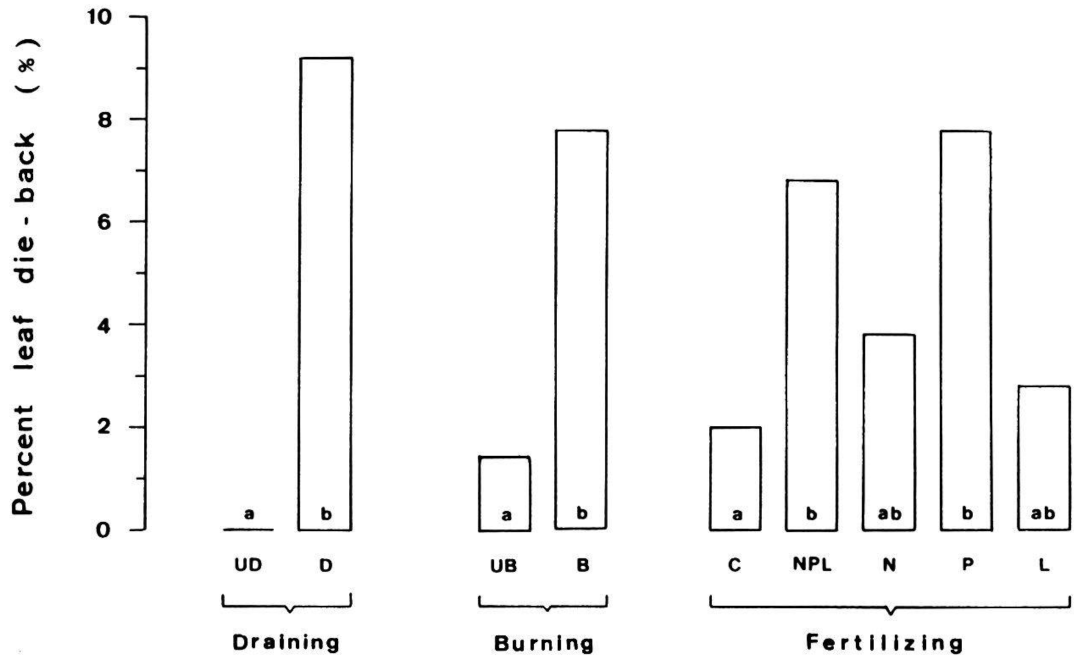


Fig. 32. Susceptibility of Typha glauca to drought: Leaf die-back on June 19 in percent of total plant height, under different draining, burning and fertilizer treatments. **Draining treatments:** UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at P<0.05 (unplanned pairwise comparisons).

regard to draining and burning regimes showed significant differences among the five treatments (P<0.001) (Table 3). Percent leaf die-back in P- and NPL-treatment plots was with 7.8 and 6.8%, respectively, significantly greater than in unfertilized plots with 2.0% (P<0.001). N- and L-treatments, on the other hand, were with 3.8 and 2.8%, respectively, not markedly different from the unfertilized C-plots (Fig. 32, Appendix 18, Table 3).

Since there were significant draining x burning (P<0.03) and draining x fertilizer (P<0.001) interactions, the two draining treatments were analysed separately (Table 3). However, because burning and fertilizer treatments did not affect susceptibility to drought in the undrained treatments (Table 3), a more detailed discussion of the data is given only for the drained treatment plots (Fig. 33, Table 4).

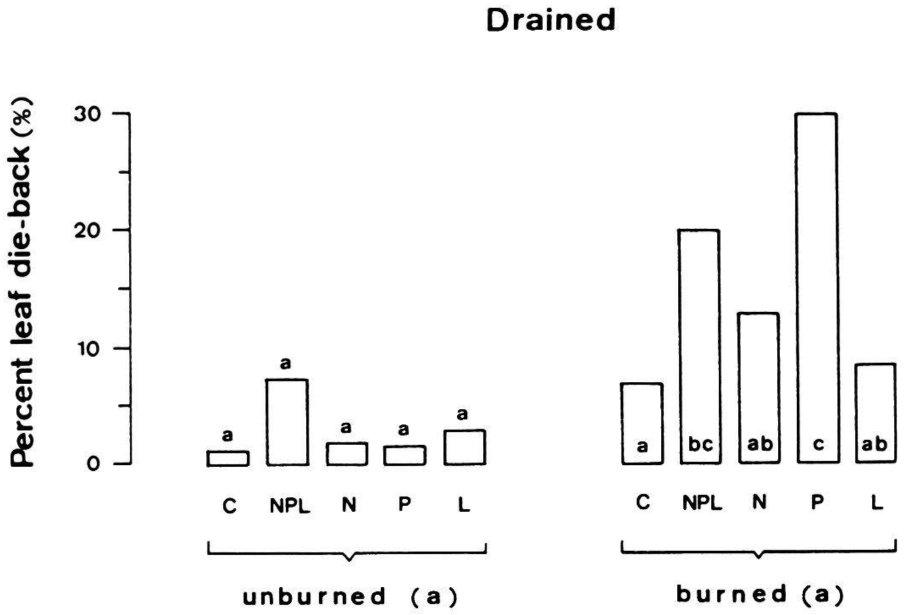


Fig. 33. Susceptibility of Typha glauca to drought in the drained basin: Leaf die-back on June 19 in percent of total plant height, in response to different fertilizer treatments which were superimposed on two burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 5. Two burning means (all fertilizer treatments combined, n = 25) and two fertilizer means within a single burning regime (n = 5) sharing the same letter are not significantly different at P<0.05 (unplanned pairwise comparisons).

Under drained conditions, the effect of the fertilizer treatments was found to depend on the burning regime, the burning x fertilizer interaction being highly significant (P<0.01) (Table 3). Unburned and burned treatment plots were, therefore, dealt with separately (Fig. 33, Table 4).

Under drained but unburned conditions, only the combined application of nitrogen, phosphorus and lime resulted in a substantial but not quite significant increase in percent leaf die-back relative to unfertilized treatments (7.3 vs. 1.1%; P<0.06) whereas the effect of adding only one of the fertilizers was negligible (Fig. 33, Table 4, Appendix 18).

Under drained and burned conditions, on the other hand, already application of only one of the fertilizers increased significantly susceptibility to drought (contrast C vs. N, P, L: P<0.05), and the difference between plots where nitrogen, phosphorus and lime had been added in combination and those where only one of them had been applied was much less

Table 4. Susceptibility of Typha glauca to drought in the drained basin: Leaf die-back (in cm and in percent of total shoot height) relative to total shoot height, shoot density and shoot standing crop on June 19 under different burning and fertilizer treatments.
C = no fertlizer added (control), N = nitrogen added, P = phosphorus added. L = lime added, NPL = nitrogen, phosphorus and lime added.

Parameters	Fertilizer treatment				
	Mean (n=25)	C (n=5)	NPL+N+P+L treatments combined (n=20)	NPL (n=5)	N+P+L treatments combined (n=15)
Unburned					
Leaf die-back (cm)	1.3	0.5	1.5	3.1	1.0
Leaf die-back (%)	2.9	1.1	3.3	7.3	2.0
Total shoot height (cm)	38.2	36.9	38.5	36.8	39.1
Shoot density (shoots/m^2)	15.8	11.7	16.9	14.5	17.7
Shoot standing crop (g dry weight/m^2)	13.5	8.5	14.8	13.5	15.2
Burned					
Leaf die-back (cm)	4.8	2.1	5.5	5.2	5.6
Leaf die-back (%)	15.6	6.9	17.7	19.9	17.0
Total shoot height (cm)	23.5	19.5	24.5	21.3	25.6
Shoot density (shoots/m^2)	13.2	9.6	14.1	15.1	13.8
Shoot standing crop (g dry weight/m^2)	3.7	2.9	3.8	4.2	3.7

pronounced (19.9 vs. 17.0%; contrast NPL vs. N, P, L: n.s.) (Fig. 33, Table 4). Leaf die-back was highest in P- and NPL-treatments with 29.7 and 19.9%, respectively, followed by N-, L- and C-treatments with 12.8, 8.4 and 6.9% (Fig. 33, Appendix 18).

It is argued that the greater water requirements in the burned plots were due to the hotter microclimatic conditions in burned as compared to unburned treatments. This, since on June 19 percent leaf die-back was much more important in burned plots despite smaller shoot height ($P<0.02$) and shoot density (n.s.) and, in consequence, smaller aboveground biomass ($P<0.05$) and transpiring surface per unit area in burned as compared to unburned treatment plots (Tables 3 and 4, Appendices 4, 6 and 20). Taking into account smaller transpiring surface per unit area in burned treatments, the difference in water stress between burned and unburned plots was even greater than indicated by the percent leaf die-back data. The hotter microclimatic conditions were mainly due to the significantly reduced load of insulating litter in burned relative to unburned treatments (110.3 vs. 766.1 g/m^2; C- and NPL-treatments combined; $P<0.0005$) (Fig. 40, Table 3, Appendix 23) as well as to the decreased albedo of the fire-blackened surface.

The higher water requirements in the fertilized treatments, on the other hand, were due to the greater transpiring surface per unit area in the fertilized (NPL-, N-, P- and L-treatments combined) as compared to unfertilized C-treatment plots. On June 19, the fertilizer treatments had not yet increased markedly shoot height, but shoot density was greater by approximately 50% in fertilized (NPL-, N-, P- and L-treatments combined) than in unfertilized C-plots, both under burned (+46.9%; n.s.) as well as under unburned (+44.4%; n.s.) conditions (Table 4, Figs. 11 and 13). The finding that the litter load in plots fertilized with nitrogen, phosphorus and lime was higher than in unfertilized plots both under unburned (899.2 vs. 633.0 g/m^2; n.s.) as well as under burned conditions (115.4 vs. 105.2 g/m^2; n.s.) further corroborates this conclusion (Fig. 40, Appendix 23).

4.9. INSECT DAMAGE

Between the end of July and the end of September, a die-back of the inner leaves could be observed with certain *Typha* shoots. The die-back was caused by stem-boring insect larvae that had entered the shoots 10 to 20 cm above soil surface and were eating the center portion of the leaf bundle. The larvae were not identified but closely resembled in ecology and size to the larvae of *Leucania scirpicola* found by BEULE (1979) in a *Typha glauca* stand in Wisconsin.

The percentage of infested shoots seemed to be positively correlated to the wetness of the site, the heaviest infestation occurring in the undrained-unburned treatments (Figs. 34 and 35). Almost no infested shoots were observed in the drained basin (0.8%) as compared to 20.3% in the undrained basin ($P<0.0001$; all burning and fertilizer treatments combined) (Table 3, Appendix 19). On burned plots where temperatures were higher and conditions consequently somewhat drier, the percentage of infested shoots was significantly lower than in unburned plots (8.6% vs. 12.6%; P<0.01; all draining and fertilizer treatments combined). On the other hand, there were no significant differences among the five fertilizer treatments (Figs. 34 and 35, Table 3, Appendix 19).

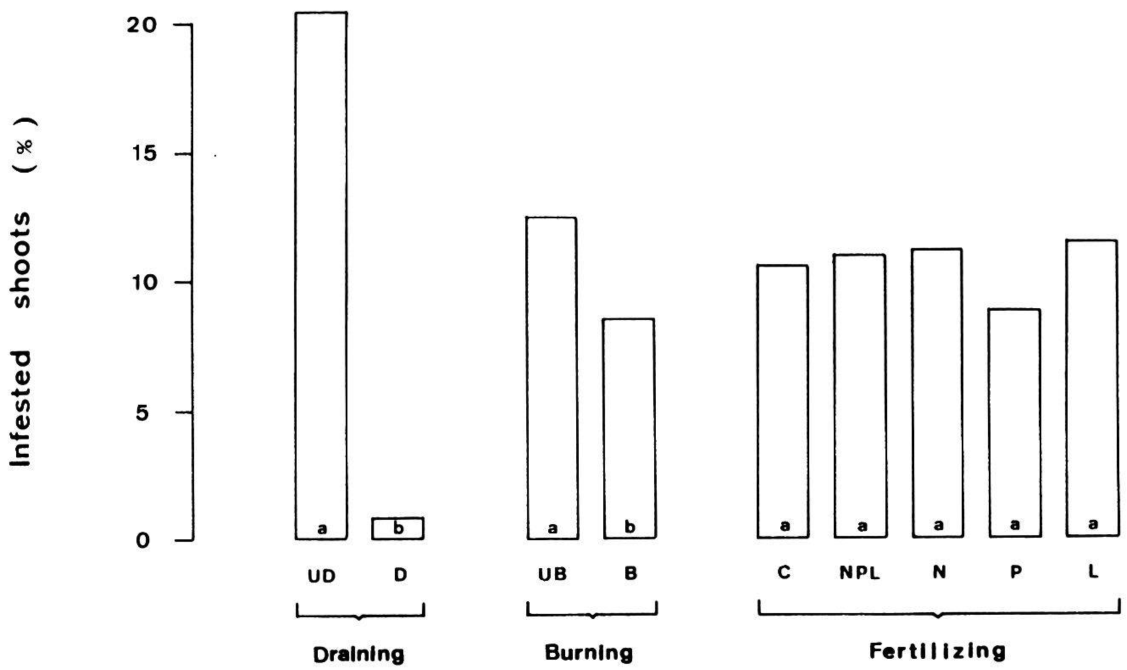


Fig. 34. Insect damage: Percentage of Typha glauca shoots attacked by stem-boring insect larvae, under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at P<0.05 (unplanned pairwise comparisons).

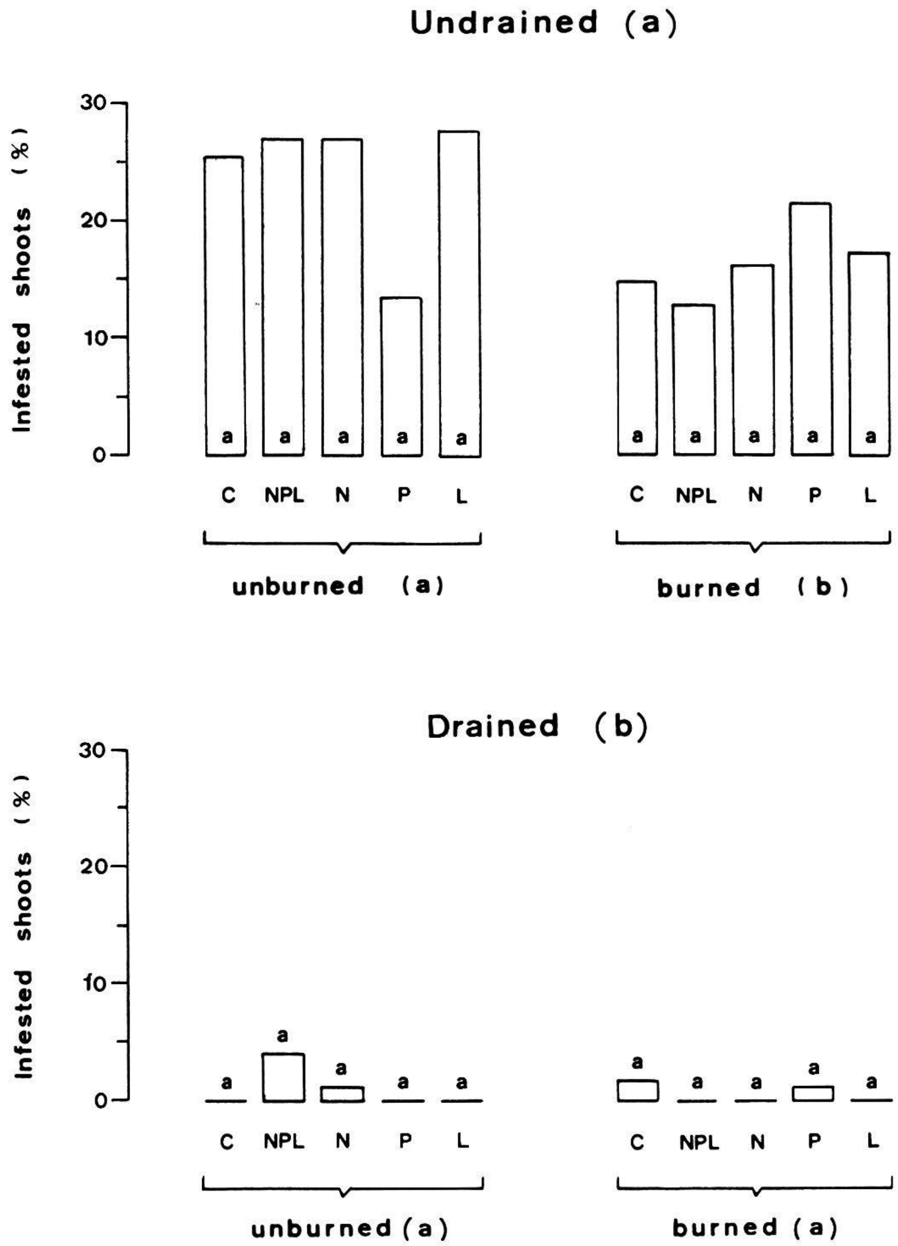


Fig. 35. Insect damage: Percentage of <u>Typha glauca</u> shoots attacked by stem-boring insect larvae, in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 5. Two draining means (all burning and fertilizer treatments combined; n = 50), two burning means within a single draining regime (all fertilizer treatments combined, n = 25) and two fertilizer means within a single draining x burning regime (n = 5) sharing the same letter are not significantly different at P<0.05 (unplanned pairwise comparisons).

4.10. ABOVEGROUND STANDING CROP

4.10.1. Typha shoot standing crop

As mentioned above Typha shoot standing crop was measured in C- and NPL-treatment plots only. For N-, P- and L-plots shoot standing crop (S) was predicted by multiple regression, using the means of final shoot height (H), final shoot density (D), basal shoot circumference (C) and number of leaves per shoot (L) as predictor variables. The regression equation was: $\ln(S) = -7.5417+1.2549*\ln(H)+0.9624*\ln(D)+1.4997*\ln(C)-0.8836*\ln(L)$, the four variables together explaining 95.2% of the variance ($P<0.025$), mean final shoot height alone accounting for 86.0% ($P<0.001$) and together with final shoot density for 94.2% ($P<0.001$). This is consistent with the findings of BOYD (1971) who reported for Typha latifolia that shoot standing crop was more closely related to average shoot weight (which is a function of shoot height) than to the average number of shoots per unit area. Figure 36 shows the relation between shoot standing crop and

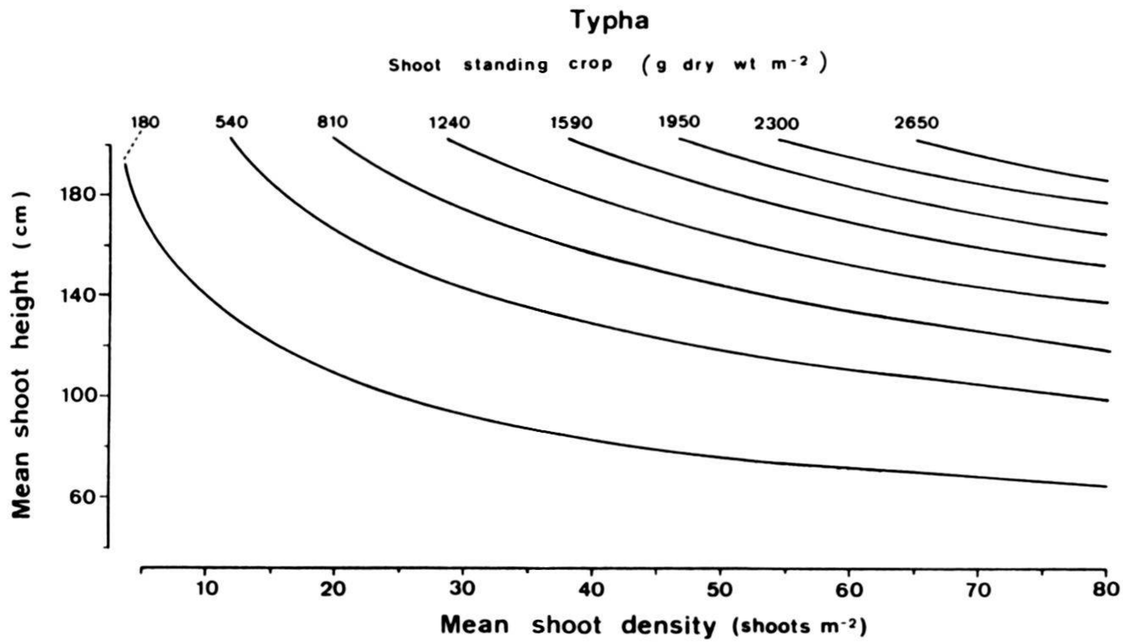


Fig. 36. Shoot standing crop (S) of Typha glauca (g dry weight/m^2) as predicted from mean shoot height (H) and mean shoot density (D) (contour plot). The regression equation $\ln(S) = -9.26288 + 2.4953*\ln(H) + 0.93681*\ln(D)$ explained 94.2% of the variance ($P<0.001$).

mean shoot height and density for the range of mean heights and densities observed in the present study. As regards draining, burning and NPL-fertilizer treatments, results of the analysis of variance tests were the same whether or not values estimated by multiple regression were included.

On the whole, the standing crop data corroborated the pattern revealed by the other Typha growth parameters measured (Table 3). However, the response of the shoot standing crop to the different treatments was in general much more marked than that of the other parameters. Shoot standing crop proved to be particularly responsive to draining as well as to fertilizing with nitrogen alone or in combination with phosphorus and lime (Figs. 37 and 38).

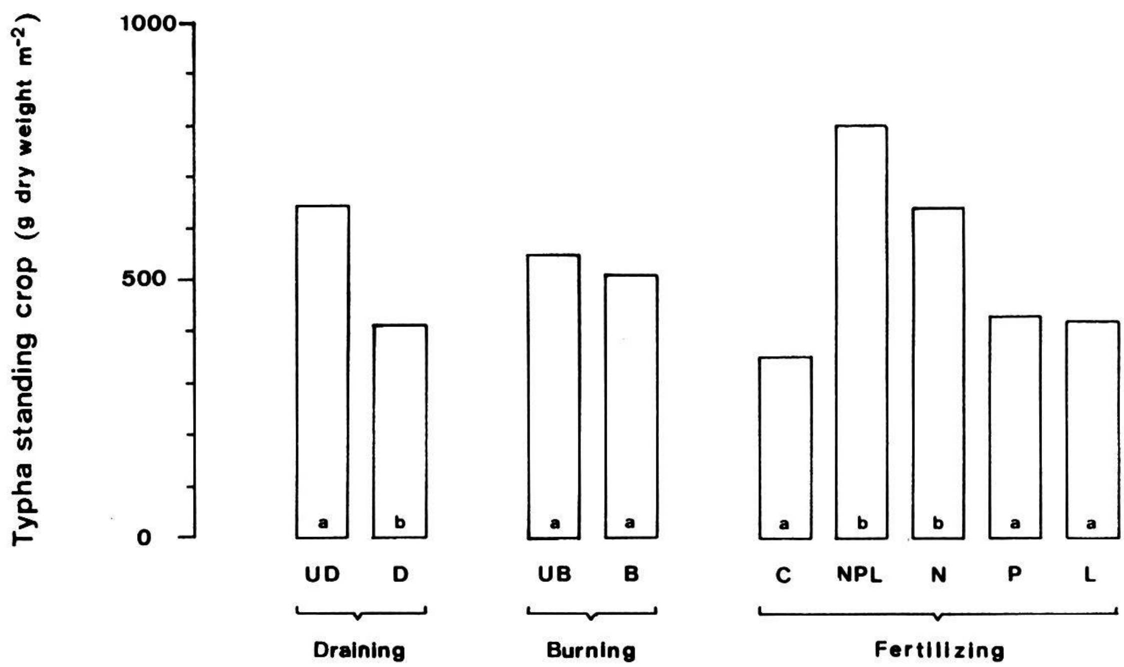


Fig. 37. Shoot standing crop of Typha glauca (g dry weight/m^2) under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer treatments combined. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; n = 20; all draining and burning treatments combined. Two draining, burning or fertilizer treatment means sharing the same letter are not significantly different at P<0.05 (unplanned pairwise comparisons).

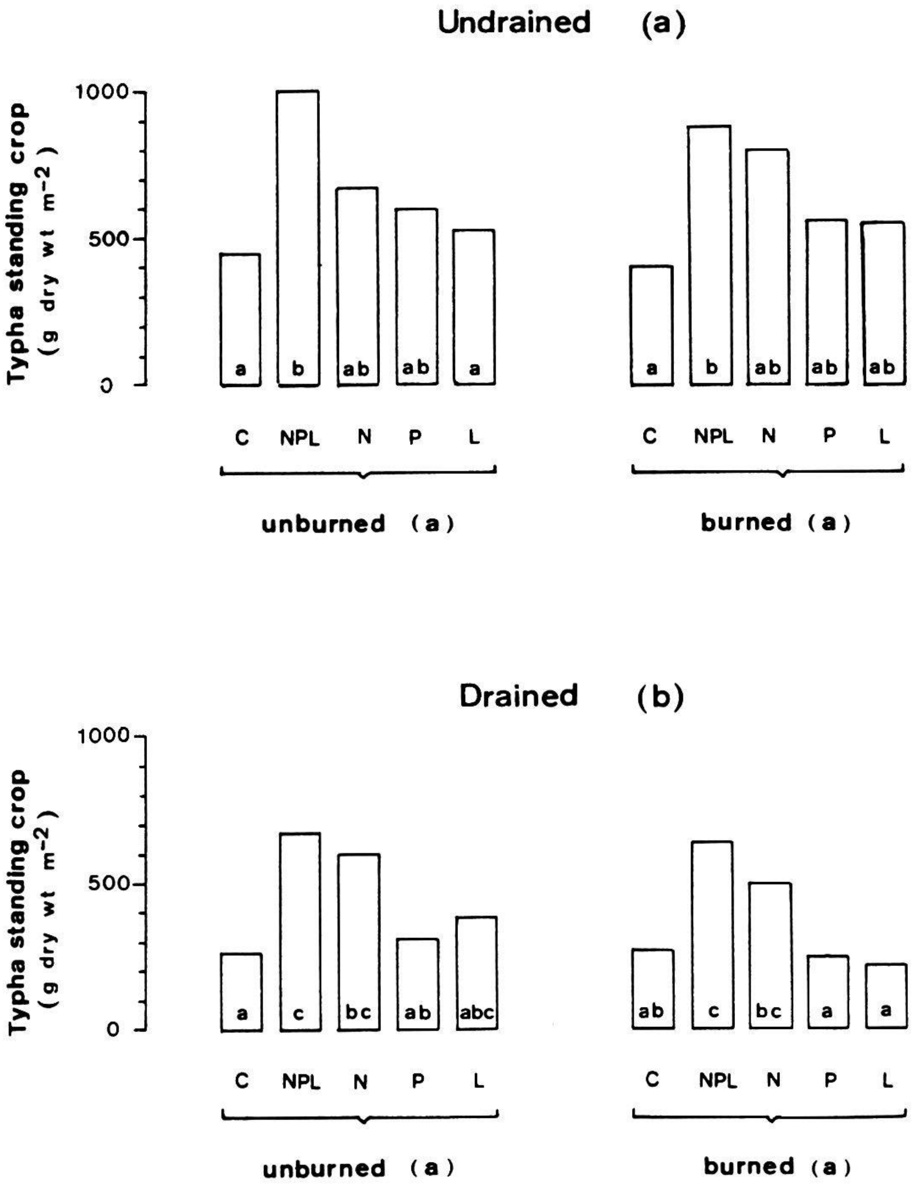


Fig. 38. Shoot standing crop of Typha glauca (g dry weight/m^2) in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; $n = 5$. Two draining means (all burning and fertilizer treatments combined; $n = 50$), two burning means within a single draining regime (all fertilizer treatments combined, $n = 25$) and two fertilizer means within a single draining x burning regime ($n = 5$) sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons).

Draining reduced shoot standing crop to 63.6% of that in undrained treatments (410.2 vs. 644.6 g/m^2; all burning and fertilizer treatments combined; P<0.004) (Fig. 37, Table 3, Appendix 21). Spring burning, on the other hand, did not significantly reduce Typha shoot standing crop (Table 3). Draining and fertilizer treatments combined, Typha shoot standing crop amounted in burned plots to 92.4% of that in unburned ones (506.5 vs. 548.3 g/m^2; n.s.). As would be expected, the impact of burning was more pronounced in the drained (374.5 g/m^2 in burned vs. 445.9 g/m^2 in unburned plots; all fertilizer treatments comined; n.s.) than in the undrained basin (638.4 vs. 650.7 g/m^2; n.s.) (Fig. 38, Table 3, Appendix 21).

As regards the fertilizer treatments, global evaluation of the data with no regard to draining x burning regimes showed that Typha shoot standing crop differed significantly among the five treatments (P<0.0001) (Fig. 37, Table 3). Shoot standing crop was highest in NPL- and N-fertilized plots with 800.1 g/m^2 (231.4% of the value in unfertilized plots) and 642.0 g/m^2 (185.7%), respectively, followed by P-, L- and unfertilized C- plots with 427.5 g/m^2 (123.7%), 421.8 g/m^2 (122.0%) and 345.7 g/m^2 (100.0%), respectively (Fig. 37, Appendix 21). The difference between unfertilized and NPL- and N-plots, respectively, was highly significant (P<0.0001) (Table 3). When the distinction was made only between fertilized (NPL, N, P, L) and unfertilized (C) treatments, fertilizer impact was practically the same under the two draining (undrained: +65.6%, drained: +65.8%; both burning treatments combined) as well as under the two burning regimes (unburned: +69.1%, burned: +62.3%; both draining treatments combined) (Fig. 38).

In contrast to final shoot height, basal shoot circumference and number of leaves per shoot (Figs. 15, 16, 18, 20, Appendices 7-9), the difference in shoot standing crop between NPL- and N-treatment plots was not greater under burned (761.0 vs. 647.8 g/m^2; both draining treatments combined) than under unburned conditions (839.2 vs. 636.2 g/m^2) (Fig. 38, Appendix 21). The reduced shoot dimensions in nitrogen fertilized plots of the burned treatments were apparently compensated for by reduced shoot densities in the respective unburned plots (Figs. 9 and 10, Appendices 3 and 4).

Addition of phosphorus tended to increase Typha shoot standing crop in the undrained basin (580.2 g/m^2 vs. 422.7 g/m^2 in unfertilized plots; both burning treatments combined; n.s.) as well as in the drained-unburned treatments (306.8 vs. 262.6 g/m^2; n.s.) but seemed to reduce it in drained burned plots (242.8 vs. 274.7 g/m^2; n.s.) (Fig. 38, Appendix 21).

Likewise, liming increased standing crop somewhat under undrained (543.3 g/m^2 vs. 422.7 g/m^2 in unfertilized plots; both burning treatments combined; n.s.) as well as under drained-unburned conditions (384.3 vs. 262.6 g/m^2; n.s.) but decreased it in the drained-burned treatments (216.3 vs. 274.7 g/m^2; n.s.) (Fig. 38, Appendix 21).

4.10.2. Aboveground standing crop of plants other than *Typha*

The aboveground standing crop produced by plants other than *Typha* was much lower than that produced by *Typha*. In the undrained basin, it amounted on average to 50.0 g dry weight per square meter (range: 0.0 to 180.4 g), that is 7.8% of the *Typha* shoot standing crop (range: 0.0 to 23.0%); in the drained basin, the respective values were 10.0 g/m^2 (range: 0.0 to 70.4 g), that is 2.4% (range: 0.0 to 8.8%) (Figs. 38 and 39, Appendices 21 and 22). The difference between the two draining treatments was significant ($P<0.05$; all burning and fertilizer treatments combined) (Fig. 39, Table 3).

Burning affected the aboveground standing crop of plants other than *Typha* differently in the two draining treatments, the draining x burning interaction being highly significant ($P<0.0004$). In the undrained basin, it was significantly higher in unburned than in burned plots (93.2 vs. 6.8 g/m^2; $P<0.001$; fertilizer treatments combined), whereas there was no significant difference between unburned and burned treatments in the drained basin (5.6 vs. 14.4 g/m^2; n.s.) (Fig. 39, Table 3, Appendix 22).

As regards the fertilizer treatments, data were gathered only in unfertilized C-plots and in plots fertilized with nitrogen in combination with phosphorus and lime (NPL-plots). There was, however, no consistent pattern (Fig. 39). Combined addition of phosphorus, nitrogen and lime affected the shoot standing crop of plants other than *Typha* differently in the two draining regimes (draining x fertilizer interaction: $P<0.04$), and differently in the two burning treatments within the drained and almost differently between those of the undrained basin (burning x fertilizer interactions: $P<0.02$ and $P<0.058$, respectively) (Table 3). Means and significance of differences are shown in Figure 39 and in Appendix 22.

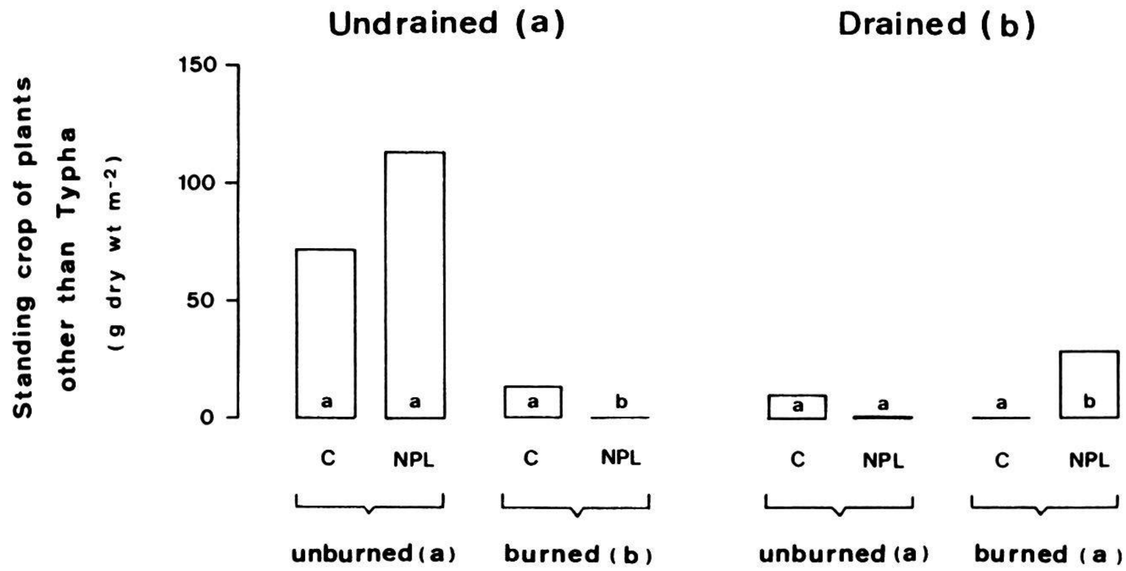


Fig. 39. Aboveground standing crop of plants other than Typha (g dry weight/m^2) under two different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; n = 5) Two draining means (all burning and fertilizer treatments combined; n = 20), two burning means within a single draining regime (all fertilizer treatments combined, n = 10) and two fertilizer treatment means within a single draining x burning regime (n = 5) sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons).

4.10.3. Litter load

In contrast to the standing crop of plants other than Typha, the litter load was rather more important in quantity than Typha shoot standing crop (Figs. 38 and 40, Appendices 21 and 22). In the unburned and unfertilized plots of the undrained basin, it amounted on the average to 569.3 g dry weight/m^2 (range: 436.4 to 705.2 g/m^2), that is 128.3% of the Typha shoot standing crop (range: 79.5 to 240.8%); in the drained basin, the respective values were 633.0 g/m^2 (range: 365.6 to 855.6 g/m^2) and 241.6% (range: 152.8 to 304.9%).
The actual litter load in gram dry weight per square meter was not significantly higher in the drained than in the undrained basin (633.0 vs. 569.3 g/m^2; unburned and unfertilized plots only). In comparison with

<u>Typha</u> shoot standing crop (100%), however, the amount of litter in the drained basin (241.6%) was significantly more important than that in the undrained one (128.3% (one-tailed t-Test: $P<0.01$), indicating a slower rate of surface litter decomposition in the drained basin (Figs. 37, 38, 40, Appendices 21 and 23).

As would be expected, the litter load was significantly lower in burned as compared to unburned treatments (170.6 vs. 684.9 g/m^2; $P<0.0001$; all draining and fertilizer treatments combined). Fire impact was more pronounced in the drained (110.3 vs. 766.1 g/m^2 in unburned plots;

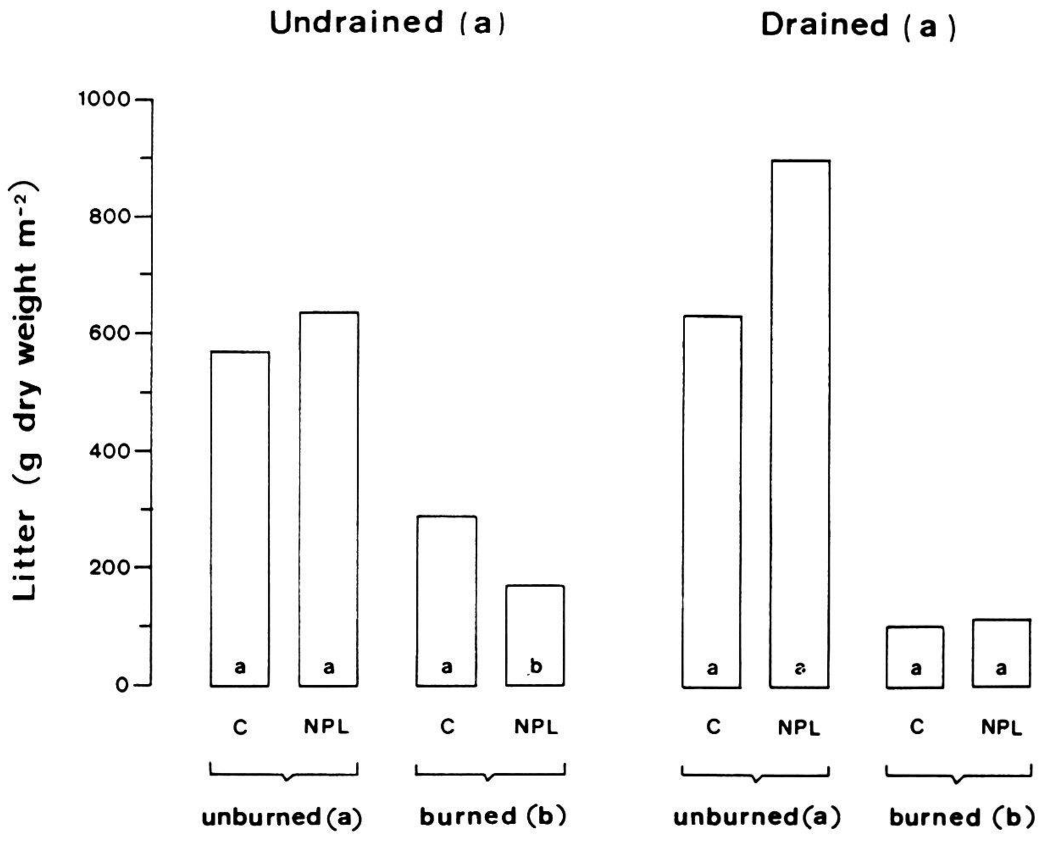


Fig. 40. Litter load (g dry weight/m^2) under two different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; n = 5) Two draining means (all burning and fertilizer treatments combined; n = 20), two burning means within a single draining regime (all fertilizer treatments combined, n = 10) and two fertilizer treatment means within a single draining x burning regime (n = 5) sharing the same letter are not significantly different at $P<0.05$ (unplanned pairwise comparisons).

$P<0.0005$; fertilizer treatments combined) than in the undrained treatments (230.8 vs. 603.6 g/m^2; $P<0.0004$), the difference between undrained-burned and drained-burned plots being highly significant ($P<0.007$; fertilizer treatments combined) (Fig. 40, Table 3, Appendix 23).

For estimating the amount of litter removed by burning, however, only the unfertilized treatment plots should be considered, since in the undrained basin the litter load differed significantly between burned-fertilized and burned-unfertilized plots ($P<0.02$). In the unfertilized plots of the drained basin, burning had reduced the litter load by 83.4% (105.2 vs. 633.0 g/m^2; $P<0.0002$) whereas the reduction in the undrained basin amounted to only 49.1% (290.0 vs. 569.3 g/m^2; $P<0.01$). The difference between the amount of litter in undrained-burned and drained-burned treatment plots was highly significant ($P<0.002$; unfertilized treatments only).

As regards the fertilizer treatments, the combined application of nitrogen, phosphorus and lime affected the litter load not in the same way in all four draining x burning regimes (burning x fertilizing interaction: $P<0.05$) (Fig. 40, Table 3). Under undrained and burned conditions, the amount of litter was significantly reduced in NPL-fertilized plots (171.6 vs. 290.0 g/m^2 in unfertilized plots; $P<0.04$). In the other three draining x burning regimes, by contrast, the litter load was always somewhat higher on fertilized than on unfertilized plots, the difference between the two treatments being almost significant under the drained x unburned regime (899.2 vs. 633.0 g/m^2; ($P<0.06$) (Fig. 40).

It can be inferred from the data that surface litter decomposed less rapidely in the drained treatments, and there less rapidly in fertilized than in unfertilized plots. Since the litter load tended to be higher in fertilized plots, the slower rate of decomposition in the drained basin was probably due to lack of moisture. In the undrained basin, on the other hand, low temperatures in combination with lack of nutrients were probably limiting, since only the combination of burning and fertilizing resulted in a reduced litter load (Fig. 40, Appendix 23).

5. DISCUSSION

Whereas results are arranged according to the different *Typha* growth parameters measured, the discussion summarizes the impact of the treatments on *Typha* from the viewpoint of the three main treatments viz. (i) draining, (ii) burning and (iii) fertilizing, followed by conclusions encompassing an evaluation of the paludification-fire-nutrient release hypothesis formulated by WEIN (1983).

5.1. DRAINING

Draining was expected to render the microclimate warmer, improving thereby nutrient supply as well as nutrient uptake by roots (e.g. DOWDING 1981). The interaction between soil temperature and nutrient uptake is well known (e.g. NIELSON 1971, MORRIS 1980, McGILL et al. 1981) and has been demonstrated for agricultural crops (see e.g. HEWITT and SMITH 1974), for arctic and alpine plant communities (e.g. McCOWN 1973, 1978, CHAPIN 1978, TRANQUILLINI 1982) as well as for salt (e.g. MORRIS 1982) and freshwater marshes (McNAUGHTON 1966, ADRIANO et al. 1980, SHARITZ et al. 1984).
McNAUGHTON (1966) found the height of *Typha latifolia* and *Typha domingensis* growth in a controlled environment to be generally greater at higher temperatures, both daytime as well as nighttime temperatures being important. ADRIANO et al. (1980) showed for *Typha latifolia* in a greenhouse experiment that growth and nutrient uptake were enhanced more by elevation of soil temperatures within the range of 18 to 32^{o}C than by addition of nitrogen or phosphorus. *Typha* shoot biomass was 1.7 and 2.2 times greater at soil temperatures of 25 and 32^{o}C, respectively, than at 18^{o}C. SHARITZ et al. (1984) reported for *Typha latifolia* and *Typha domingensis* growing in a thermally graded nuclear reactor reservoir in South Carolina that elevated water temperatures tended to enhance growth and uptake of macronutrients, corroborating the findings of McNAUGHTON (1966) and ADRIANO et al. (1980) obtained under controlled conditions.

PRENTKI et al. (1978) reported for Typha latifolia that rates of phosphorus uptake were 5.5 times higher at 20°C as compared to 5°C. Unlike the macronutrients, uptake of micronutrients appeared not to be enhanced by elevated water temperatures (ADRIANO et al. 1984).
Moreover, warmer microclimatic conditions are generally assumed to increase the rate of decomposition (e.g. GODSHALK and WETZEL 1978b, McGILL et al. 1981, BRINSON et al. 1981, POLUNIN 1982), thereby making nutrients previously locked up in surface litter and soil organic matter available to plants. This has been reported for arctic plant communities (e.g. BLISS et al. 1973, WIDDEN 1977, WEBBER 1978) but also for temperate freshwater ecosystems (e.g. PAUL et al. 1978, KLOPATEK 1978, POLUNIN 1984). In addition, draining can be expected to improve the redox conditions in the rooting zone allowing, in turn, again faster decomposition (e.g. GODSHALK and WETZEL 1978b), greater nutrient uptake (e.g. LINTHURST 1979, 1980, MORRIS 1980, HOWES et al. 1981, VALIELA et al. 1982) and enhanced plant growth (e.g. MENDELSSOHN et al. 1982).
Assuming improved nutrient uptake and increased rate of decomposition in drained treatments, moderate draining was expected to lead to taller plants and greater standing crop. However, this was not found to be the case (Table 5). Lowering the water table from soil surface to an average of ca. 28 cm below ground reduced Typha shoot standing crop to 64% of that in undrained plots. The reduction was due to both smaller shoot dimensions (shoot height -9.4%, basal shoot circumference -8.1%, number of leaves per shoot -0.6%) and reduced density (-17.6%). In addition, shoot emergence started 11.0 days later under drained conditions and senescence was complete 14.7 days earlier. In consequence, draining shortened the duration of the assimilation periods 0% and 50% by 13.4% and 20.6%, respectively. Susceptibility to drought was much more pronounced under drained conditions (percent leaf die-back on June 19: 9.2% in the drained vs. 0% in the undrained basin) whereas damage caused by stem-boring insect larvae was drastically reduced (-96.1%). The litter load, in contrast, was somewhat greater (+5.0%) in the drained treatments.

Only little work has hitherto been undertaken on the effects of draining on cattail. BEULE (1979) reported that during drawdown in a Wisconsin Typha glauca stand stem density decreased by 36% from 42 to 27 shoots per square meter; the impact of the drawdown on shoot dimensions was not specified. BEULE (1979) emphasized, however, that once established, cat-

Table 5. The effect of lowering the water table from soil surface to an average of 28.4 cm below ground on biometric characteristics of Typha glauca (all burning and fertilizer treatments combined). Values are differences to the undrained treatment. If differences are given in days, minus stands for earlier and plus for later.
Significance symbols (planned orthogonal comparisons):
* = P<0.05, ** = P<0.01, *** = P<0.001, NS = P>0.06
°) 9.2% in drained vs. 0% in undrained treatments

Parameter	Difference drained vs. undrained	
1) Start of shoot emergence	+11.0 days	***
2) Shoot density on June 12	-61.0%	***
3) Shoot density on June 19	-31.9%	**
4) Shoot density on June 19 in percent of final shoot density	-17.2%	*
5) Final shoot density	-17.6%	NS
6) Shoot height on June 19	-46.6%	***
7) Final shoot height	- 9.4%	*
8) Basal shoot circumference	- 8.1%	*
9) Number of leaves per shoot	- 0.6%	NS
10) Length of the assimilation period 0%	-13.4%	***
11) Length of the assimilation period 50%	-20.6%	***
12) Start of the assimilation period 0%	+ 6.8 days	***
13) Start of the assimilation period 50%	+ 9.8 days	***
14) Day after May 15 on which shoot height reached 71.1 cm	+14.1 days	***
15) Duration of senescence 50% (yellowing halfway through)	-12.5 days	***
16) Duration of senescence 100% (yellowing complete)	-14.7 days	***
17) Green height in percent of total height on October 3	-39.4 days	***
18) Susceptibility to drought (percent leaf die-back on June 19)	+ ∞ % °)	***
19) Insect damage (percent infested shoots)	-96.1%	***
20) Typha shoot standing crop on June 19	80.2%	***
21) Typha shoot standing crop in Oct./Nov.	-36.4%	**
22) Standing crop of plants other than Typha in Oct./Nov.	-80.0%	*
23) Litter load in Oct./Nov.	+ 5.0%	NS

tails can endure periods of dry soils or deep flooding and persist under constantly changing water levels. That Typha has the capability to recover quickly from disturbances such as draining and burning and combinations thereof has also been shown by KRüSI and WEIN (1988). Consistent with our findings for Typha glauca, HASLAM (1970) reported for another freshwater macrophyte, Phragmites communis, that a sudden fall in the water level reduced shoot height and delayed shoot emergence and maturation. In contrast, however, to our findings as well as to the reports of BEULE (1979) and KRüSI and WEIN (1988) with Typha glauca, HASLAM observed Phragmites communis shoot density to be sometimes higher (HASLAM 1971a) and sometimes lower (HASLAM 1971c) in drier than in wetter biotopes, depending on the competitors present on a given site. In agreement with the response of Typha glauca in the present experiment, MOOK and VAN DER TOORN (1982) and VAN DER TOORN and MOOK (1982) observed in a field experiment with Phragmites communis reduced shoot standing crop, thinner shoots and a lower percentage of plants infested by stem- boring insect larvae under dry as compared to wet conditions.

It could be argued that lack of water was limiting Typha growth in the drained basin. That water supply can be insufficient in the drained treatments became apparent during a three week long spell of low rainfall conditions at the beginning of the vegetation period; leaves began to wilt, became yellow and died back at the tips on an average of 9.2% of the total shoot height at the time. However, extended drought periods are rare in Atlantic Canada and there was no further evidence of severe water stress during the remainder of the vegetation period.
The fertilizer experiments showed that occasionally poor water supply was not the only and probably not the main cause of the reduced Typha growth observed in the drained treatments. Enrichment with nitrogen alone or in combination with phosphorus and lime lead to almost the same plant height in both the drained and the undrained treatments, indicating nitrogen as the primary factor limiting Typha growth.
The observation that senescence of leaves proceeded faster in drained as compared to undrained treatments and that addition of nitrogen slowed down the process of yellowing is consistent with the hypothesis that growth in the drained treatments is limited by lack of nutrients rather than by lack of water. In cereal grasses, the symptoms of nitrogen deficiency are known to include not only chlorosis, narrowing of leaves and

tip burn but also more rapid senescence of leaves (e.g. GREGORY 1937, CHAPMAN 1966, MENGEL and KIRKBY 1978, THIMANN 1980, MEI and THIMANN 1984). MORRIS (1982) reported for Spartina alterniflora a linear, positive correlation between nitrogen and chlorophyll concentration of leaves and a significantly reduced rate of senescence in plants well supplied with nitrogen. In the present study nitrogen fertilized plants were easily recognizable by their dark green colour, indicating high chlorophyll concentrations in leaves.
The more rapid shoot death observed in the drained treatments might also have been caused by frost. In addition to senescence and drought, also freezing may lead to shoot death, often referred to as frost-drought (see e.g. TRANQUILLINI 1982 for bibliography). At soil surface, subzero temperatures occurred, in fact, as much as five to six weeks earlier in the drained as compared to the undrained basin (KRüSI and WEIN 1982).
However, since addition of nitrogen proved to slow down the process of senescence under drained conditions to the levels observed in the undrained treatments, frost can be excluded as crucial factor. According to McGILL et al. (1981) shoot death due to freezing is related to temperatures in the canopy rather than at soil surface. Microclimatic measurements with help of the sucrose inversion method (e.g. LEE 1969, JONES and COURT 1980) showed no significant differences in the canopy temperatures between the two draining treatments (KRüSI unpubl.).

Given that the crucial factor limiting growth in the drained treatments is lack of nutrients rather than lack of water, the question arises whether (i) the nutrients are still locked up in the surface litter and in soil organic material or whether (ii) they are dissolved in the interstitial water but can, nevertheless, not be taken up by plants due to other limiting factors (e.g. MORRIS 1980, MENDELSSOHN et al. 1982, VALIELA et al. 1982).
The combination of higher litter load by simultaneously lower shoot production leads to the conclusion that surface litter decomposes more slowly in the drained than in the undrained treatments. It could be argued that this is due to (i) differences in the chemical composition of the litter or to (ii) different temperature and moisture conditions in the two draining treatments.
It is known that the rate of decomposition can vary significantly between but also within species in function of e.g. plant age, plant

parts, site conditions and year (see e.g. McGILL et al. 1981, BRINSON et al. 1981 and POLUNIN 1984 for bibliography). Decomposability of litter is generally considered to depend on the C : N (e.g. HUNT 1977, McGILL et al. 1981) and the lignin : carbohydrate ratio (e.g. HERMAN et al. 1977). This dependence was found to hold true also for litter of freshwater macrophytes (e.g. DAVIS and VAN DER VALK 1978a, GODSHALK and WETZEL 1978a, BRINSON et al. 1981, POLUNIN 1982, 1984, SHAVER and MELILLO 1984). For Typha latifolia a significant positive correlation between environmental levels of nutrients and their concentration in live as well as dead plant tissues was found under controlled (BOYD 1971, SHAVER and MELILLO 1984) as well as under natural (BOYD and HESS 1970, KLOPATEK 1978) conditions. The slower rate of decomposition in the drained treatments could, therefore, indicate poorer nutrient supply in drained as compared to undrained treatments.

The observation that in drained conditions the litter load in plots fertilized with nitrogen, phosphorus and lime was even higher than in unfertilized ones strongly suggests, on the other hand, that in the drained basin lack of moisture was limiting decomposition of surface litter rather than a possibly less favourable chemical composition of the dead plant material. It is argued that fertilizing brought about drier site conditions by the salt effect as well as by the increased transpiration due to greater biomass and transpiring surface per unit area.

This conclusion is consistent with the higher susceptibility to drought observed in the fertilized as compared to the unfertilized treatments in the drained basin. The findings of POLUNIN (1982) who reported increased actual decomposition of Phragmites australis litter when nitrogen and phosphorus were added, corroborates further the conclusion that decomposition of surface litter in the drained treatments was primarily limited by lack of moisture.

According to BRINSON et al. (1981), there is contradictory evidence as to whether rates of decomposition in freshwater wetlands are higher under dry or under wet conditions. SHARMA and GOPAL (1982) reported no significant differences in the rate of decomposition of Typha elephantina litter under dry and submerged conditions in India. However, POLUNIN (1984) concludes in his review paper that permanently submerged macrophyte litter typically decomposes more rapidly than litter which is intermittently inundated or kept largely dry. This conclusion is consistent with our findings.

Soil organic matter, on the other hand, was found to decompose more rapidly under drained than undrained conditions (KRüSI unpubl.). This was expected since draining leads to increased air space and accelerated soil warming in the surface layers, conditions conducive to high rates of decomposition (e.g. GODSHALK and WETZEL 1978b, DOWDING 1981).
In addition to the rate of decomposition, also nitrogen fixation is likely to be affected by draining. Evidence as to whether draining increases or decreases nitrogen fixation is, however, contradictory, since there is a considerable range of organisms capable of nitrogen fixation over a wide range of oxygen tensions, and little is known about their temperature and moisture requirements (DOWDING 1981).
It is concluded that, on the whole, nutrient supply was comparable in quantity under both draining regimes, since the reduced rate of surface litter breakdown in the drained treatments was probably compensated for by the more rapid decomposition of soil organic matter.
Nevertheless, shoot standing crop of Typha in the drained treatments did not reach the levels observed under undrained conditions, neither in unfertilized nor in fertilized plots. Given Typha growth in the drained treatments being limited by lack of nutrients rather than by lack of water, and nutrient supply being comparable under both draining conditions, reduced Typha growth in the drained treatments could be due to lower rates of nutrient uptake caused by changes in the microclimate related to draining.
Microclimatic measurements showed that temperatures were much more extreme in the drained than the undrained basin, hotter during the day and cooler at night. At soil surface the mean weekly temperature amplitudes recorded throughout the vegetation period were 24.6 ±1.3 (1 S.E., n = 21) °C and 12.8 ±0.8°C for drained and undrained treatments, respectively. Exponential mean temperatures as measured by the sucrose inversion method (e.g. LEE 1969, JONES and COURT 1980), on the other hand, were higher in drained than in undrained treatments only above the ground but neither at soil surface nor in the soil. At soil surface, exponential mean temperatures recorded for the periods June 12 to July 12 and July 14 to October 4, respectively, were the same for both draining treatments. At 2, 10 and 20 cm belowground, finally, exponential mean temperatures were found to be lower in the drained as compared to the undrained basin. At a depth of 10 cm, that is where the main bulk of the Typha rhizomes was located, the exponential mean temperatures measured in the

unburned and unfertilized plots of the drained and undrained treatments were 11.2 ±0.3 (1 S.E., n = 10)°C vs. 13.8 ±0.1°C for the period of June 12 to July 12 and 21.0 ±1.4°C vs. 23.6 ±0.9°C for the period of July 14 to October 4, respectively. The higher mean soil temperatures in the undrained as compared to the drained treatments were most likely due to the high heat storage capacity of water, resulting in a much lower heat loss during the night in the undrained as compared to the drained treatments. The significant delay in shoot emergence observed in the drained basin is consistent with the cooler soil temperatures recorded there.

The contrary to expectation cooler mean temperatures in the rooting zone of Typha in the drained basin, could very well be the reason why Typha shoot standing crop in the drained treatments did not reach the levels observed in the undrained basin, neither in unfertilized nor in fertilized plots. As discussed above, Typha growth and nutrient uptake is highly dependent on soil temperature and generally greater at higher temperatures (McNAUGHTON 1966, ADRIANO et al. 1980, SHARITZ et al. 1984).

However, it could also be argued that the reduced shoot production found in the drained treatments was compensated for by increased root and rhizome production, overall standing crop being the same in both draining treatments. McNAUGHTON (1966), for instance, reported for Typha angustifolia grown in a controlled environment, that night temperatures affected the root/shoot ratio but not overall production. Since belowground standing crop was not estimated in the present study, it can not be excluded that overall standing crop was in fact the same in both draining treatments. But even if that were the case, a higher root/shoot ratio in the drained treatments itself would indicate less favourable conditions in drained than in undrained plots, high root/shoot ratios being generally considered to be an adaptive response of plants to harsh environmental conditions (e.g. DAVIDSON 1969, MOONEY 1972, HUNT 1975). This has been found to hold true for a variety of ecosystems (e.g. KUCERA et al. 1967, SHAVER and BILLINGS 1975, VALIELA et al. 1976, SMITH et al. 1979, MORRIS 1982, HOPKINSON and SCHUBAUER 1984). For Typha latifolia grown under controlled conditions, BOYD (1971), SZCZEPANSKA (1976) and SHAVER and MELILLO (1984) observed the root/shoot ratio to decrease with increasing soil fertility, and McNAUGHTON (1966) reported root/shoot ratios in natural stands of Typha latifolia to decrease along a North to South transect from North Dakota to Texas.

It is concluded that reduced *Typha glauca* growth in the drained as compared to the undrained treatments was primarily caused by the lower mean soil temperature in the rooting zone of *Typha*, and secondarily only by occasional lack of water, the cooler soil temperatures resulting, in turn, in poorer uptake of nutrients and reduced growth (ADRIANO et al. 1980). The comparatively cooler soil temperatures were, furthermore, most likely responsible for the marked delay in shoot emergence under drained as compared to undrained conditions. Lack of moisture, on the other hand, seemed to be the primary cause for the reduced rate of surface litter decomposition observed in the drained treatments; and improved soil aeration was responsible for the more rapid break down of soil organic matter in the drained as compared to the undrained basin.

5.2. BURNING

Fire can affect distribution and cycling of nutrients in ecosystems directly and indirectly. Directly by (i) heating and possibly killing living organisms aboveground as well as in the upper soil layers, (ii) addition of ash to the soil surface, (iii) loss of nutrients through volatilization and as particulate matter in the smoke; and indirectly by changing controlling abiotic factors viz. (i) availability of nutrients (post-fire nutrient pulse, H-ion concentration) and (ii) microclimatic conditions (temperature, water, light) which, in turn, influence the nutrient status of the system by affecting the rate of decomposition as well as the nutrient uptake (e.g. RAISON 1979, WOODMANSEE and WALLACH 1981, WRIGHT and BAILEY 1982, CHANDLER et al. 1983, MacLEAN et al. 1983). It goes without saying, that degree and magnitude of the abovementioned fire effects depend on fire intensity as well as on the season of burning (e.g. WRIGHT and KLEMMEDSON 1965, TRABAUD and LEPART 1981, TRABAUD 1983, TOWNE and OWENSBY 1984, KRüSI and WEIN 1988).

In general, burning has been reported to increase the amount of available nutrients, and changes in microclimatic conditions brought about by fire are generally considered to be favourable for plant growth; removal of vegetation and surface litter as well as decreased albedo of the fire-blackened soil surface, lead typically to elevated post-fire soil temperatures enhancing, in turn, the rate of nutrient uptake, the rate of decomposition and possibly the rate of nitrogen fixation (see e.g. RAISON 1979, WOODMANSEE and WALLACH 1981, WRIGHT and BAILEY 1982, CHANDLER et al. 1983, MacLEAN et al. 1983 for bibliography). Elevated post-fire temperatures in combination with a ready supply of nutrients in the ash were found to be particularly conducive to high rates of decomposition (e.g. HOFSTEN and EDBERG 1972, POLUNIN 1982, 1984). It comes, therefore, as no surprise that reports of increased plant production after fire are numerous (see e.g. MacLEAN et al. 1983 for bibliography). Some of the most dramatic increases in plant growth were reported for Australian "ashbed" sites, where they were comparable to increases found when "luxury" doses of nitrogen and phosphorus fertilizers were applied (RAISON 1979).

In both the undrained and the drained basin, burning was carried out on the same day. The phenological development of <u>Typha glauca</u> was, however, not the same on that day for the two draining treatments. In the undrained basin, already 37% of the shoots had emerged and they had reached approximately 21% of their final height whereas the respective values for the drained basin were 5% and 10% only. Direct damage to <u>Typha</u> was, therefore, most likely more severe in undrained than in drained plots. Fire intensity, in contrast, was more extreme in the drained treatments due to higher fuel load in combination with lower fuel moisture. In the drained treatments, approximately 85% of the surface litter was consumed as compared to about 50% in the undrained treatments. Loss of nutrients through volatilization as well as indirect fire effects such as, for instance, pulse addition of nutrients and increase in soil temperatures etc. were, thus, expected to be much more pronounced in the drained treatments.
Given greater direct damage during the fire and smaller post-fire benefits, that is smaller amount of locked-up nutrients released, smaller increase in soil temperatures etc., <u>Typha</u> growth was expected to increase less dramatically in undrained-burned than in drained-burned treatments. However, no such increase in <u>Typha</u> productivity was observed in the present study, neither in the drained nor in the undrained basin. Burning did not significantly alter current years <u>Typha</u> shoot standing crop (Table 6). The slight reduction of standing crop observed (-7.6%) was entirely due to smaller shoot dimensions in the burned as compared

Tab. 6. The effect of spring burning superimposed on two draining regimes on biometric characteristics of <u>Typha glauca</u> in the year of burning (all fertilizer treatments combined). Values are differences to the unburned treatment. If differences are given in days, minus stands for earlier and plus for later.
Significance symbols (planned orthogonal comparisons):
(*) = P<0.06, * = P<0.05, ** = P<0.01, *** = P<0.001,
NS = P>0.06

o) Taking into account only the unfertilized treatments burning reduced the litter load by 67.1% (both draining treatments combined), 49.1% (undrained treatments only) and 83.4% (drained treatments only), respectively.

Parameter	Difference burned vs. unburned		
	Both draining treatments	Undrained treatments only	Drained treatments only
1) Start of shoot emergence	Shoot emergence started before plots were burned		
2) Shoot density on June 12	+ 59.1% **	+ 21.6% NS	+400.0% **
3) Shoot density on June 19	- 1.1% NS	+ 10.4% NS	- 16.5% NS
3) Shoot density on June 19 in percent of the final shoot density	- 9.7% NS	+ 1.4% NS	- 21.7% NS
5) Final shoot density	+ 11.1% NS	+ 11.8% NS	+ 11.9% NS
6) Shoot height on June 19	- 33.3% ***	- 30.5% **	- 38.5% *
7) Final shoot height	- 8.6% (*)	- 5.8% NS	- 11.7% NS
8) Basal shoot circumference	- 6.0% NS	- 5.5% NS	- 6.9% NS
9) Number of leaves per shoot	- 2.2% NS	- 6.7% NS	+ 2.5% NS
10) Length of the assimilation period 0%	- 7.0% ***	- 10.1% ***	- 3.5% NS
11) Length of the assimilation period 50%	- 4.0% **	- 6.3% *	- 1.2% NS
12) Start of the assimilation period 0%	+ 14.8 days ***	+ 19.0 days ***	+ 10.5 days **
13) Start of the assimilation period 50%	+ 7.6 days ***	+ 9.0 days **	+ 6.0 days **
14) Day after May 15 on which shoot height reached 71.1 cm	+ 10.9 days ***	+ 10.8 days ***	+ 10.9 days *
15) Duration of senescence 50% (yellowing half-way through)	+ 3.5 days **	+ 2.0 days NS	+ 5.2 days *
16) Duration of senescence 100% (yellowing complete)	+ 3.8 days *	+ 2.0 days NS	+ 5.6 days (*)
17) Green height in % of total height on October 3	+ 18.4% *	+ 4.1% NS	+ 46.9% NS
18) Susceptibility to drought (percent leaf die-back on June 19)	+457.1% *	0.0% NS	+437.9% (*)
19) Insect damage (percent infested shoots)	- 31.8% **	- 31.2% *	- 46.2% NS
20) Typha shoot standing crop on June 19	- 60.0% **	- 57.1% *	- 72.6% *
21) Typha shoot standing crop in Oct./Nov.	- 7.6% NS	- 1.9% NS	- 16.0% NS
22) Standing crop pf plants other than Typha in Oct./Nov.	- 78.5% **	- 92.7% ***	+157.1% NS
23) Litter load in Oct./Nov. o)	- 75.1% ***	- 61.8% ***	- 85.6% ***

to the unburned treatments (shoot height -8.6%, basal shoot circumference -6.0%, number of leaves per shoot -2.2%) and would have been more substantial, had it not been for the somewhat higher shoot density (+11.1%) in the burned plots. Under undrained conditions, the reduced shoot dimensions in the burned treatments were almost completely compensated for by the higher shoot density, Typha shoot standing crop being only 1.9% smaller in burned as compared to unburned plots; under drained conditions, on the other hand, the compensation was only partial, Typha shoot standing crop being a considerable though not significant 16% smaller in the burned treatments. Burning delayed both the start (+14.8 and +7.6 days) and the end (+3.5 and +3.8 days) of the assimilation periods 0% and 50%, reducing their duration (-7% and -4%). Burning increased markedly the susceptibility to drought under drained (+438%) but did not affect it under undrained conditions. The percentage of shoots infested by stem-boring insect larvae, on the other hand, was substantially lower in the burned treatments (-31.8%). As would be expected, burning brought about a significant reduction in the litter load (-75.1%).

Although burning is a common practice in many cattail marshes (BEULE 1979, WELLER 1982), experimental studies concerning the impact of fire on Typha are rare (KRÜSI and WEIN 1988). There is, however, some information on the response to burning of Phragmites communis, another rhizomatous freshwater macrophyte with a similar growth habit and the ability to form large monospecific stands (HASLAM 1971a,b,c, VAN DER TOORN and MOOK 1982, THOMPSON and SHAY 1985). Typically, burning of Phragmites communis L. in springtime was found to lead to smaller shoots and denser stands (HASLAM 1971a,b,c, VAN DER TOORN and MOOK 1982, MOOK and VAN DER TOORN (1982), THOMPSON and SHAY 1985). It has been shown that Phragmites shoots whose apical meristem was killed were replaced by several thinner shoots, regardless of the cause of damage, be it fire, frost, cutting or insects (SKUHRAVY 1978, VAN DER TOORN and MOOK 1982, MOOK and VAN DER TOORN 1982, 1985, THOMPSON and SHAY 1985). As regards stem-boring insect larvae, VAN DER TOORN and MOOK (1982) observed burning to reduce substantially the percentage of Phragmites shoots attacked by stem- or rhizom-boring insect larvae. These observations on Phragmites communis are consistent with the findings of the present experiment with Typha glauca. In contrast to the present experiment where burning did not significantly alter Typha shoot standing crop, MOOK and VAN DER TOORN (1982) and THOMPSON and SHAY (1985) found spring burning to increase the aerial shoot biomass of Phragmites communis by on average 70% (range: 10-135%, n=8) and approximately 50%, respectively. In both studies, the marked increase in aboveground shoot standing crop was accompanied by a significant burning-induced increase in belowground biomass by on average 50% (range: 15-110%) and approximately 70%, respectively. According to MOOK and VAN DER TOORN (1982) the burning-induced increase in shoot biomass was to a considerable part due to the fact that burning in spring reduced markedly the losses in yield caused by stem- and rhizome-boring insect larvae.

In contrast to the burned treatments where Typha shoot standing crop was not higher but, on the contrary, slightly lower than in unburned ones, a dramatic increase in Typha shoot standing crop was observed in plots where nitrogen, phosphorus and lime had been added. Shoot standing crop was there more than twice as high as in the unfertilized plots. There was no significant difference in the standing crop of NPL-fertilized plots between burned and unburned treatments. It was, therefore, concluded that (i) the direct fire damage killing already emerged shoots was not very severe and has no direct effect on the amount of shoot biomass produced, a conclusion which is consistent with the findings of MOOK and VAN DER TOORN (1982) with Phargmites, and (ii) that the nutrients previously locked-up in surface litter and released through fire and made available to plants were insufficient in quantity to stimulate Typha growth.
There are three possible explanations for this. First, it could be argued that the amount of nutrients locked-up in the surface litter was negligible due to plant internal translocation of nutrients to belowground parts during senescence. Second, the nutrient content of the surface litter was substantial but most of the nutrients were lost during the fire through volatilization or as particulate matter in the smoke, or immediately after the fire through leaching or surface run-off. Third, there was a considerable amount of nutrients in the surface litter and they were to a large extent released and deposited in the ash layer, but plants could, nevertheless, not make use of them since they were immobilized, or because fire related changes in abiotic environmental factors hampered nutrient uptake.

As for the nutrient content of freshwater macrophyte litter, several studies show that typically the major part of the aboveground nutrient standing crop is not translocated belowground in autumn (e.g. CHAPIN et al. 1975, KLOPATEK 1975, BERNARD and SOLSKY 1977, RICHARDSON et al. 1978, BERNARD and FITZ 1979, BERNARD and HANKINSON 1979, VAN DER LINDEN 1980). For Typha latifolia in a lakeshore marsh, it has been shown that 77% of the phosphorus (PRENTKI et al. 1978) and 75% of the nonstructural carbohydrates (GUSTAFSON 1976) remained on the marsh surface as litter or leachate, only the rest being translocated belowground in autumn. SHAVER and MELILLO (1984) studied the nitrogen and phosphorus recovery from dying leaves of Typha latifolia in a growth chamber study, where towards the end of the experiment daylength as well as daytime and nighttime temperatures were reduced in order to simulate transition from summer to autumn. At the end of the experiment, the mean nitrogen and phosphorus concentrations of dead leaves amounted for a range of nutrient treatments to 51.1% (range: 35.0% to 67.5%) and 55.5% (range: 25.2% to 83.8%), respectively, of that in mature green leaves; the efficiency of nitrogen and phosphorus recovery decreased with increasing availability of N and P in the nutrient solution. The differences between the values reported by PRENTKI et al. (1978) and those calculated from the data given by SHAVER and MELILLO (1984) can be attributed to the reportedly high availability of phosphorus in the marsh studied by PRENTKI et al. (1978), and/or to the different methods of calculation used, leaching not being taken into account for the values based on the data from SHAVER and MELILLO (1984).
In the present study, the litter load corresponded to 128% and 242% of one year's Typha shoot standing crop on unburned and unfertilized treatment plots in the undrained and the drained basins, respectively. The amount of nutrients released through burning was, therefore, probably considerable, even when high efficiency of nutrient recovery is assumed, taking into account their poor availability on the site studied.

Little work has hitherto been undertaken on nutrient losses to the atmosphere during burning of freshwater marshes. VAN DER LINDEN (1980) estimated for a highly productive stand of Phragmites communis the loss of nitrogen via volatilization during burning of surface litter in early spring to approximately 90 kg/ha; that is about 45% of the nitrogen accumulated aboveground during the vegetation period. This value is well within the range of 25 of 60% reported by MacLEAN et al. (1983) in their review paper as typical for temperate regions. Losses through volatilization of nutrients other than nitrogen were generally observed to be much lower, considerably more than 50% being typically returned to the soil surface from incinerated vegetation und litter (see e.g. WOODMANSEE and WALLACH 1981, WRIGHT and BAILEY 1982, CHANDLER et al. 1983, MacLEAN et al. 1983). And burning over moist soil, as was the case in the present study, should decrease losses of nitrogen and other nutrients to the atmosphere (DEBANO et al. 1979).

Loss of nutrients from ash through wind, surface run-off or leaching was most likely negligible in the present study since the organic mat remained largely unaffected by the fire and Typha plants resumed growth immediately after burning. According to BOYD (1971), Typha latifolia absorbs macronutrients at a proportionally greater rate early in the season, a pattern that has been reported for other emergent macrophytes in temperate climate (see PRENTKI et al. 1978 for bibliography) as well as for numerous other plant species (e.g. CHAPIN 1980). Furthermore, it is difficult to perceive why leaching should have affected only nutrients added in form of ash but not those added in form of fertilizers, since only 5 mm of rain were recorded during the ten days between burning and application of fertilizers as compared to 43.9 mm for the ten days following fertilizing.

It is, thus, concluded that most of the nutrients released by burning were not lost through volatilization or leaching. Assuming burning to have freed a considerable amount of nutrients which to a large extent were not lost through volatilization, run-off or leaching, the absence of increased Typha shoot production in burned plots relative to unburned ones must, in consequence, be due either to fire-induced changes in the microclimate leading to lower rates of nutrient uptake, or to fire-related mechanisms making the nutrients unavailable to plants.

Microclimatic measurements carried out on the site showed that temperatures were much extremer, hotter during the day and cooler at night, in burned than in unburned plots. At soil surface, the mean weekly temperature amplitudes during the vegetation period in burned vs. unburned plots were 33.6 ±1.0 (1 S.E., n = 21) $^{\circ}$C vs. 24.6 ±1.3 $^{\circ}$C and 21.4 ±0.9 $^{\circ}$C vs. 12.8 ±0.8 $^{\circ}$C for drained and undrained treatments, respectively. During the first month following burning, exponential mean temperatures as measured with the sucrose inversion method (e.g. LEE 1969, JONES and COURT 1980) too, were higher in burned than in unburned plots, both aboveground as well as belowground. In the main rooting zone of *Typha*, that is at about 10 cm belowground, the means recorded in burned and unburned plots for the first month following burning were 12.7 ±0.2 (1 S.E., n = 10) ^{o}C vs. 11.2 ±0.3 ^{o}C for the drained and 14.1 ±0.3 ^{o}C vs. 13.8 ±0.1 ^{o}C for the undrained treatments, the difference being marked in the drained basin only. As already stated earlier, soil temperatures were generally higher in undrained than in drained treatments. During the second, third and fourth month after burning, however, exponential mean temperatures remained higher only in the drained treatments and there only above but not below the soil surface. In the undrained treatments, they were, on the contrary, somewhat lower for the whole profile, presumably due to greater heat loss during the night in burned as compared to unburned plots.

As discussed above, increased post-fire soil temperatures are known to improve nutrient uptake and plant growth (e.g. McNAUGHTON 1966, ADRIANO et al. 1980, SHARITZ et al. 1984), to increase the depth of the active soil layer (e.g. BROWN 1983), to enhance the rate of decomposition and possibly the rate of nitrogen fixation (e.g. DAUBENMIRE 1968, RAISON 1979, WOODMANSEE and WALLACH 1981, MacLEAN et al. 1983). During the first month following burning, when mean temperatures were generally higher in burned treatments, breakdown of both surface litter as well as soil organic matter was, in fact, somewhat more rapid in burned than in unburned plots (KRÜSI unpubl.). During the remainder of the vegetation period, however, rates of decomposition were no longer different for soil organic matter and slower for surface litter.

It is, therefore, concluded that changes in microclimatic conditions brought about by fire were favourable to plant growth, enhancing the rate of nutrient uptake rather than reducing it. That burning, nevertheless, did not increase *Typha* shoot standing crop could be attributed to processes making the nutrients released through burning at least temporarily unavailable to plants (immobilization).

Such temporary immobilization of nutrients was, for instance, reported by LLOYD (1971) who observed in herbaceous vegetation in Britain increased foliar content of nitrogen and phosphorus in the second and third season following burning but not in the first. And VALIELA et al.

(1982) found in a salt marsh that Spartina alterniflora responded to fertilizing with nitrogen and phosphorus only after a lag time of one year.

In the present study, temporary immobilization of nutrients after burning could partly have been due to the observed higher post-fire rates of decomposition. High rates of decomposition are not necessarily synonymous with high rates of mineralization and ready supply of nutrients. Decomposition studies have shown that nitrogen in organic matter is mineralized only if the C:N ratio is less than about 20:1; organic matter with a higher ratio exerts, in contrast, a nitrogen demand on the soil and causes temporary immobilization of nitrogen in decomposer biomass (e.g. ENWEZOR 1976). The C:N ratio of Typha latifolia litter calculated by PRENTKI et al. (1978) based on data from BOYD (1970) was with 52:1 well above the immobilization limit. Thus, the faster the rate of decomposition the higher the nutritional demands of the associated microorganisms. As indicated by several studies, immobilization of nitrogen is sometimes accompanied by the immobilization of other nutrients, namely phosphorus (e.g. BARSDATE and PRENTKI 1973, HODKINSON 1975, DAVIS and VAN DER VALK 1978b, SHARMA and GOPAL 1982).

However, there was no evidence that temporarily immobilized nutrients became available in burned plots during the second season following burning. Typha shoot standing crop was also in the second season after fire the same in both burned and unburned treatments; Typha growth characteristics too, did, on the whole, not change from the first to the second season after fire, shoot dimensions remaining smaller and shoot densities greater in the burned treatments (KRÜSI and WEIN 1988). There was, however, one major difference. In contrast to the first season following burning when senescence proceeded somewhat more slowly in burned than in unburned plots, it proceeded in the second season after fire much more rapidly in burned as compared to unburned treatment plots. As discussed above, this indicates that in the second season after burning supply of nitrogen was poorer in burned than in unburned plots.

Furthermore, no timelag was observed in the present study between application of fertilizers and Typha response. Since it is difficult to perceive why only nutrients added through ash should have been immobilized but not those added through fertilizers, it is concluded that the amount of nutrients transferred to the ash layer was after all only sufficient to compensate for the damage inflicted upon shoots already emerged at the time of burning but insufficient to stimulate further Typha growth. However, since in the present stuy belowground standing crop of Typha was not measured, it could be argued that by stimulating belowground production, burning in springtime did, nevertheless, lead to an increase in overall standing crop of Typha. There are at least three reasons why this is very unlikely. First, higher belowground production in the first year following burning would be expected to lead, in turn, to higher aboveground production in the second year after burning, which was clearly not the case in the present experiment (KRüSI and WEIN 1988). Second, MONK and VAN DER TOORN (1982) found in their work with Phragmites that burning in springtime enhanced both belowground and aboveground production, shoot and rhizome biomass being typically closely correlated. Third, an exclusive stimulation of belowground production would lead to an higher root/shoot ratio, which has been shown to indicate a decrease rather than an increase in available nutrients (BOYD 1971, SZCZEPANSKA 1976, SHAVER and MELILLO 1984).

It is concluded that, unlike fertilizing, spring burning did not result in increased Typha shoot standing crop, the higher shoot densities observed in the burned plots being compensated for by reduced shoot dimensions. The nutritional effect of ashes in combination with higher mean soil temperatures and more rapid decomposition during the first month following fire were apparently not sufficient to stimulate Typha growth. This is consistent with the observation reported by many researchers that in grassland, as opposed to forest and scrub vegetation, the nutritional effect of ash is generally insufficient to stimulate plant growth (e.g. LLOYD 1971, see e.g. DAUBENMIRE 1968 and WRIGHT and BAILEY 1982 for bibliography).

5.3. FERTILIZING

The aboveground standing crop of current year's Typha growth of 443.9 ±83.3 (1 S.E., n = 5) g/m^2 and of 262.6 ±19.6 g/m^2 for unburned and unfertilized treatments in the undrained and drained basins, respectively, are very low when compared with values reported in the literature. This was possibly due to the unique habitat conditions, Typha growing on a floating organic mat with no direct contact to the mineral soil. VAN DER VALK and DAVIS (1978b) found for Typha glauca in Iowa season's maximum shoot standing crops ranging from 758 to 2118 g/m^2 with an average of 1156 g/m^2. And shoot standing crops reported by other authors were, in increasing order, 946 g/m^2 in central Minnesota (BERNARD and BERNARD 1973), 1320 g/m^2 in New Jersey (WHIGHAM and SIMPSON 1976), 1360 g/m^2 in Minnesota (BRAY 1962), 1361 g/m^2 in central New York (BERNARD and FITZ 1979), 1565 g/m^2 in New Jersey (JARVIS 1969) and 1680 g/m^2 in Minnesota (BRAY et al. 1959).

Aboveground standing crops reported for other Typha species in North America viz. T. latifolia, T. angustifolia and T. domingensis ranged from 378 g/m^2 for Typha latifolia in South Dakota (McNAUGHTON 1966) up to 4040 g/m^2 for Typha angustifolia in Czechoslovakia (DYKYJOVA 1971) (see GUSTAFSON 1976, WHIGHAM et al. 1978, BRINSON et al. 1981 for reviews). Since Typha shoot production on the site studied was by far the lowest ever reported for Typha glauca and among the lowest reported for other Typha species, fertilizing was expected to increase Typha growth considerably.

Nitrogen, phosphorus and lime. The combined application of nitrogen, phosphorus and lime resulted, in fact, in a highly significant 2.31-fold increase in Typha shoot standing crop. The higher aboveground standing crop of current year's Typha growth was due to both greater shoot dimensions and higher shoot densities (Table 7). In plots fertilized with nitrogen in combination with phosphorus and lime, shoots were by the end of the vegetation period 27% taller in height, 42.7% thicker in diameter and had 24.4% more leaves than shoots in unfertilized plots, and there

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Table 7 (page 91). The effect of the combined addition of **nitrogen** (200 kg/ha), **phosphorus** (200 kg/ha) **and lime** (625 kg/ha) on biometric characteristics of Typha glauca under different draining x burning regimes. Values are differences to the unfertilized treatment. If differences are given in days, minus stands for earlier and plus for later.
Significance symbols (planned orthogonal comparisons):
(*) = P<0.06, * = P<0.05, ** = P<0.01, *** = P<0.001,
NS = P>0.06
(1) = 4.0% in NPL-fertilized vs. 0% in unfertilized plots
(2) = 28.8 g dry weight/m^2 in NPL-fertilized vs. 0 g in unfertilized plots

Parameter	Difference NPL-fertilized vs. unfertilized				
	All draining and burning treatments combined	Undrained treatments only		Drained treatments only	
		unburned	burned	unburned	burned
1) Start of shoot emergence	← Start of emergence before fertilizers were added →				
2) Shoot density on June 12	← Application of fertilizers on June 13 →				
3) Shoot density on June 19	+ 7.5% NS	- 9.4% NS	- 6.1% NS	+ 23.9% NS	+ 57.3% NS
4) Shoot density on June 19 in percent of final shoot density	- 9.2% NS	- 23.5% NS	- 29.4% *	+ 4.3% NS	+ 47.3% NS
5) Final shoot density	+ 22.4% NS	+ 16.2% NS	+ 38.2% NS	+ 2.3% NS	+ 31.0% NS
6) Shoot height on June 19	0.0% NS	- 0.6% NS	- 3.8% NS	- 0.3% NS	+ 9.2% NS
7) Final shoot height	+ 27.0% ***	+ 13.2% NS	+ 28.6% ***	+ 28.7% ***	+ 41.0% ***
8) Basal shoot circumference	+ 42.7% ***	+ 25.3% *	+ 54.0% ***	+ 44.4% ***	+ 49.1% **
9) Number of leaves per shoot	+ 24.4% ***	+ 13.2% (*)	+ 24.7% **	+ 23.7% **	+ 37.2% ***
10) Length of the assimilation period 0%	+ 5.2% **	+ 4.8% NS	+ 8.4% **	+ 4.7% NS	+ 2.7% NS
11) Length of the assimilation period 50%	+ 2.2% NS	+ 1.3% NS	+ 3.5% NS	+ 2.7% NS	+ 1.6% NS
12) Start of the assimilation period 0%	← Start of AP 0% before fertilizers were added →				
13) Start of the assimilation period 50%	+ 5.0 days ***	+ 2.9 days NS	+ 7.5 days *	+ 5.4 days *	+ 4.3 days NS
14) Day after May 15 on which shoot height reached 71.1 cm	- 3.1 days (*)	- 0.1 days NS	- 1.5 days NS	- 3.7 days NS	- 7.1 days NS
15) Duration of senescence 50% (yellowing halfway through)	+ 7.2 days ***	+ 4.3 days NS	+ 11.0 days **	+ 7.7 days *	+ 5.7 days NS
16) Duration of senescence 100% (yellowing complete)	+ 7.3 days ***	+ 7.9 days NS	+ 12.2 days **	+ 6.7 days NS	+ 2.2 days NS
17) Green height in percent of total height on October 3	+ 29.3% ***	+ 11.7% NS	+ 36.2% *	+ 61.3% *	+ 24.6% NS
18) Susceptibility to drought (percent leaf die-back on June 19)	+240.0% ***	0.0% NS	0.0% NS	+563.6% NS	+188.4% **
19) Insect damage (percent infested shoots)	+ 4.2% NS	+ 6.0% NS	- 14.0% NS	+ ∞ (1) NS	-100.0% NS
20) Typha shoot standing crop on June 19	- 2.9% NS	- 12.1% NS	- 6.7% NS	+ 58.8% NS	+ 44.8% NS
21) Typha shoot standing crop in Oct./Nov.	+131.4% ***	+126.5% **	+120.5% **	+156.3% ***	+132.0% **
22) Standing crop of plants other than Typha in Oct./Nov.	+ 47.9% NS	+ 56.0% NS	-100.0 **	- 92.3% NS	+ ∞ (2) *
23) Litter load in Oct./Nov.	+ 14.2% NS	+ 12.0% NS	- 40.8% *	+ 42.1% NS	+ 9.7% NS

were 22.4% more shoots per square meter in NPL-treatment plots. In addition, fertilizing with nitrogen, phosphorus and lime delayed the end of senescence by 7.3 days, extending the duration of the assimilation period (AP 0%) by 5.2%. The percentage of Typha shoots infested by stem-boring insect larvae was not affected by application of nitrogen in combination with phosphorus and lime. Whereas the response of the above-mentioned parameters to fertilizing did not vary significantly among the different draining x burning regimes; this was not true for shoot emergence, susceptibility to drought and litter load. Under undrained conditions, shoot emergence proceeded more slowly and was complete later in NPL-fertilized than in unfertilized plots; under drained conditions, on the other hand, shoot emergence progressed more rapidly in NPL-treatment plots but was complete at more or less the same time in both NPL-fertilized and unfertilized treatment plots. The application of nitrogen, phosphorus and lime increased the susceptibility to drought in the drained but not in the undrained basin. As regards the litter load, fertilizing with nitrogen, phosphorus and lime decreased the amount of litter in undrained-burned treatments, increased it in the drained-unburned plots and did not change it under the undrained-unburned and the drained-burned regime.

In contrast to salt marshes (see e.g. VALIELA et al. 1982, CARGILL and JEFFERIES 1984 for bibliography), there are to my knowledge no experiments where known amounts of fertilizers had been added to Typha dominated freshwater marshes in natural conditions. There are, however, numerous studies on the potential for using freshwater wetlands for wastewater treatments (see e.g. SLOEY et al. 1978, KADLEC 1980, WHIGHAM and BAYLEY 1980, VAN DER VALK et al. 1980, WHIGHAM 1982 for bibliography) but they focused primarily on efficiency of nutrient removal and not on the impact of the nutrients on macrophyte growth. In wastewater experiments it is, moreover, often hard to distinguish between the effects of the different and sometimes toxic components; comparisons with the results of the present study are, therefore, mostly not possible.
However, there are studies comparing Typha shoot standing crop and site fertility parameters (BOYD and HESS 1970, BOYD 1971, SZCZEPANSKA and SZCZEPANSKI 1976) as well as a number of growth chamber experiments addressing the response of Typha species to fertilizer treatments (BOYD 1971, SZCZEPANSKA and SZCZEPANSKI 1976, DYKYJOVA 1978, ADRIANO et al.

1980, SHAVER and MELILLO 1984). Both approaches have their drawbacks. When comparing different sites, nutrient levels will most likely not be the only variables affecting production (e.g. BOYD 1971, ADRIANO et al. 1980) and findings from greenhouse experiments are not always valid in nature (e.g. SZCZEPANSKA and SZCZEPANSKI 1976).

Under natural conditions, BOYD and HESS (1970) observed for 28 Typha latifolia stands in the southeastern United States a positive correlation between Typha shoot standing crop and environmental phosphorus and calcium levels; however, the other site fertility parameters, namely the nitrate concentration in the water, were not correlated with standing crop. Comparing five Typha latifolia stands of essentially the same low soil fertility in South Carolina BOYD (1971) found, on the other hand, a wide variation in Typha shoot standing crop, which was apparently not related to site fertility but to other site parameters; standing crop was more closely related to average shoot weight than to average shoot density. SZCZEPANSKA and SZCZEPANSKI (1976) comparing site fertility and production of six natural Typha angustifolia stands in Poland, observed likewise no consistent pattern; under natural conditions, the standing crop of T. angustifolia was found to depend mainly on shoot density and not on the weight of the individual shoots. For natural stands of Typha angustifolia in Czechoslovakian fishponds differing in the supply of available nutrient DYKYJOVA (1978), by contrast, reported that shoot standing crop was always higher on eutrophic than on oligotrophic sites.

As regards the greenhouse experiments, BOYD (1971) reported for Typha latifolia an increase in shoot density by 95%, in shoot height by 71% and in shoot standing crop by 685% when 1200 ppm of a commercial 6-12-12 N-P-K fertilizer was added to marsh soil. SZCZEPANSKA and SZCZEPANSKI (1976) grew Typha latifolia and T. angustifolia in mud from the bottom of an eutrophic lake to which different amounts of sand had been added; an increase in the amount of mud from 12.5% to 100% resulted in a 4- and 6-fold increase in the shoot standing crop of T. latifolia and T. angustifolia, respectively. In contrast to the natural stands of T. angustifolia studied where standing crop was mainly related to shoot density, in the greenhouse experiment shoot standing crop was related chiefly to the height and the weight of the shoots (SZCZEPANSKA and SZCZEPANSKI 1976). ADRIANO et al. (1980) reported an approximately 1.6 times higher total standing crop (aboveground and belowground) of Typha latifolia when 100 ppm nitrogen and 60 ppm phosphorus (based on dry soil weight) were added to the floodplain soil used as growing medium. In the so fertilized treatments the tallest leaves per shoot were 12% and the number of leaves per shoot 10% higher as compared to unfertilized ones. No data on shoot densities were given. SHAVER and MELILLO (1984) grew Typha latifolia in washed coarse sand to which different amounts of nitrogen and phosphorus were added. A 9-fold increase in the amount of nitrogen (from 0.042 to 0.375 g N per week and 7 liter pot) and phosphorus (from 0.006 to 0.055 g P per week and 7 liter pot) added resulted in a 3.2-fold higher standing crop of the shoots produced during the experiment. The authors did not specify whether the higher standing crop was due to taller and thicker shoots or greater shoot densities.

In contrast to the above-mentioned experiments, DYKYJOVA (1978) found that Typha shoot biomass declined when the amount of nutrients supplied exceeded an optimum level. DYKYJOVA (1978) grew Typha latifolia in an outdoor hydroponic culture starting from rhizome cuttings. The basic nutrient solution (100%) contained 375 mg actual nitrogen and 155 mg actual phosphorus per liter as well as micronutrients. As would be expected, Typha shoot biomass was always higher in fertilized than in unfertilized treatments. However, production reached its peak already in the 50% nutrient solution and declined when the concentrations exceeded this level; in the 200% treatment (750 mg N/liter, 310 mg P/liter), Typha shoot biomass amounted to only c. 40% of that in the 50% treatment (187.5 mg N/liter, 77.5 mg P/liter). DYKYJOVA (1978) observed the same pattern with other marsh species viz. Phragmites communis, Acorus calamus, Bolboschoenus maritimus and argues that micronutrients might have reached toxic levels in the higher concentrated nutrient solutions.

Given the marked increase in Typha shoot standing crop brought about by the combined addition of nitrogen, phosphorus and lime in the present experiment, the question arises which of the three components was the crucial one. Evaluation of the data showed that Typha glauca growth was primarily limited by lack of nitrogen and secondarily only by phosphorus and lime, as discussed in the following.

Nitrogen. Application of 200 kg/ha nitrogen resulted in a significant 1.86-fold increase in Typha shoot standing crop. In the unburned treatments, the higher standing crop was only due to greater shoot dimensions whereas in the burned treatments both larger shoot dimensions and higher shoot densities contributed to the increase (Table 8). In the unburned treatments addition of nitrogen alone (N-plots) resulted in practically the same increases in final shoot height (+18.0 vs. +20.5%), basal shoot circumference (+41.8 vs. +34.6%) and number of leaves per shoot (+22.4 vs. +18.3%) as did the combined addition of nitrogen, phosphorus and lime (NPL-plots) whereas in the burned treatments the respective increases were substantially smaller in N- than in NPL-plots (+16.0 vs. +34.3%, +27.8 vs. +51.7%, +10.7 vs. +31%). Addition of nitrogen reduced final shoot density in the unburned treatment plots (-10.2%) but increased it under burned conditions (+36.1%). The delay in the end of senescence and the prolongation of the assimilation period (AP 0%) observed in NPL-fertilized plots (+7.3 days, +5.2%) was equalled when nitrogen alone was applied (+7.9 days, +5.9%). Likewise, addition of nitrogen alone affected shoot emergence in practically the same way as did fertilizing with nitrogen in combination with phosphorus and lime. The percentage of Typha shoots attacked by stem-boring insect larvae was not significantly changed by addition of nitrogen, and susceptibility to drought remained likewise unaffected by nitrogen enrichment save for the drained-burned treatments where it was significantly increased. The litter load was not measured in nitrogen-fertilized plots. In conclusion, fertilizing with nitrogen affected Typha almost in the same way as did the combined application of nitrogen, phosphorus and lime (Tables 7 and 8).

Phosphorus. Addition of 200 kg/ha phosphorus, on the other hand, increased Typha shoot standing crop only in the undrained basin (+37.3%) but left it basically unchanged in the drained one (+2.3%). In the undrained basin the relative to unfertilized treatments higher shoot standing crop in phosphorus-fertilized plots was due to both larger shoot dimensions (height +9.5%, basal circumference +12.8%, number of leaves per shoot +6.3%) and greater shoot density (+13.1%) (Table 9). In the drained basin, on the other hand, the greater shoot density in phosophorus-fertilized plots (+15.9%) was compensated for by the smaller basal circumference of the shoots (-8.8%); final shoot height (+1.2%) and number of leaves per shoot (-0.4%) were not basically affected by the addition of phosphorus in the drained basin. Addition of phosphorus delayed the end of senescence (+6 days) and extended the duration of the assimilation period (AP 0%) (+3.9%) only under undrained conditions; under drained conditions, on the other hand, senescence was complete three

Parameter	Difference nitrogen-fertilized vs. unfertilized				
	All draining and burning treatments combined	Undrained treatments only		Drained treatments only	
		unburned	burned	unburned	burned
1) Start of shoot emergence	← Start of emergence before nitrogen was added →				
2) Shoot density on June 12	← Application of nitrogen on June 13 →				
3) Shoot density on June 19	- 3.1% NS	- 31.9% NS	- 2.8% NS	+ 23.9% NS	+ 29.2% NS
4) Shoot density on June 19 in percent of final shoot density	- 9.3% NS	- 19.3% NS	- 32.1% *	+ 17.9% NS	+ 21.1% NS
5) Final shoot density	+ 13.0% NS	- 15.2% NS	+ 44.0% NS	- 3.2% NS	+ 27.8% NS
6) Shoot height on June 19	+ 6.6% NS	- 1.8% NS	+ 4.7% NS	+ 8.9% NS	+ 33.8% NS
7) Final shoot height	+ 17.1% ***	+ 13.7% NS	+ 12.1% NS	+ 22.8% **	+ 20.5% *
8) Basal shoot circumference	+ 35.0% ***	+ 33.8% **	+ 32.6% **	+ 50.3% ***	+ 21.1% NS
9) Number of leaves per shoot	+ 16.5% ***	+ 15.2% *	+ 9.3% NS	+ 30.5% ***	+ 12.0% NS
10) Length of the assimilation period 0%	+ 5.9% ***	+ 6.2% *	+ 8.7% **	+ 2.8% NS	+ 5.7% NS
11) Length of the assimilation period 50%	+ 7.8% ***	+ 5.2% NS	+ 13.1% ***	+ 6.3% NS	+ 6.7% NS
12) Start of the assimilation period 0%	← Start of AP 0% before nitrogen was added →				
13) Start of the assimilation period 50%	+ 1.0 days NS	+ 2.1 days NS	- 1.7 days NS	+ 2.7 days NS	+ 1.0 days NS
14) Day after May 15 on which shoot height reached 71.1 cm	- 4.1 days **	- 1.6 days NS	- 5.6 days *	- 5.1 days NS	- 3.9 days NS
15) Duration of senescence 50% (yellowing halfway through)	+ 8.6 days ***	+ 8.0 days *	+ 11.6 days **	+ 8.1 days *	+ 6.7 days *
16) Duration of senescence 100% (yellowing complete)	+ 7.9 days ***	+ 10.2 days *	+ 12.6 days **	+ 3.9 days NS	+ 4.8 days NS
17) Green height in percent of total height on October 3	+ 26.9% **	+ 10.2% NS	+ 25.2% NS	+ 68.1% *	+ 25.2% NS
18) Susceptibility to drought (percent leaf die-back on June 19)	+ 90.1% NS	0.0% NS	0.0% NS	+ 63.6% NS	+ 85.5% *
19) Insect damage(percent infested shoots)	+ 6.0% NS	+ 6.5% NS	+ 9.3% NS	+ ∞ (1) NS	-100.0% (2) NS
20) Typha shoot standing crop on June 19	- 13.3% NS	- 31.6% NS	+ 5.8% NS	+ 60.0% NS	+ 37.9% NS
21) Typha shoot standing crop in Oct./Nov.	+ 85.7% ***	+ 50.7% NS	+ 97.8% *	+129.7% **	+ 82.6% *
22) Standing crop of plants other than Typha in Oct./Nov.	← no measurements →				
23) Litter load in Oct./Nov.	← no measurements →				

days earlier and the assimilation period was slightly shorter (-1.2%) in phosphorus-fertilized than in unfertilized plots. Addition of phosphorus increased the susceptibility to drought only in the drained-burned treatments (+330%) but not under the other draining x burning regimes. Addition of phosphorus resulted under all draining and burning conditions in more rapid shoot emergence. The extent of insect damage, finally, on Typha shoots, on the other hand, was not significantly influenced by phosphorus enrichment. The litter load was not measured in phosphorus-fertilized plots. On the whole, addition of phosphorus increased Typha growth to some extent in the undrained treatments but did practically not affect it in the drained ones (Table 9).

Lime. Liming at a rate of 625 kg agricultural grade lime per hectare increased Typha shoot standing crop under undrained (+28.5%) and drained-unburned conditions (+46.3%) but reduced it under drained-burned ones (-21.3%); however, in none of the four draining x burning regimes the difference in standing crop between limed and unfertilized plots was significant (Table 10). The changes in shoot standing crop brought about by liming were mainly due to alterations in shoot density (+19% in undrained, +34.7% in drained-unburned and -17.6% in drained-burned treatment plots) whereas the impact of liming on shoot dimensions was rather small (final height +2.3%, basal circumference -4%, number of leaves per shoot -1.8%; all draining and burning treatments combined). Under undrained conditions, liming did practically not affect the date on which senescence was complete (-0.9 days) and the length of the assimilation period (AP 0%) (-0.6%); under drained conditions, on the other hand, senescence was complete 6.4 days earlier and the assimilation period (AP 0%) 3.4% shorter in limed as compared to untreated plots. As was true

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Table 8 (page 96). The effect of fertilizing with **nitrogen** (200 kg/ha) on biometric characteristics of Typha glauca under four different draining x burning regimes. Values are differences to the unfertilized treatment. If differences are given in days, minus stands for earlier and plus for later.
Significance symbols (planned orthogonal comparisons):
(*) = P<0.06, * = P<0.05, ** = P<0.01, *** = P<0.001, NS = P>0.06

(1) = 1.2% in N-fertilized vs. 0% in unfertilized plots
(2) = 1.7% in N-fertilized vs. 0% in unfertilized plots

Parameter	Difference phosphorus-fertilized vs. unfertilized				
	All draining and burning treatments combined	Undrained treatments only		Drained treatments only	
		unburned	burned	unburned	burned
1) Start of shoot emergence	← Start of emergence before phosphorus was added →				
2) Shoot density on June 12	← Application of phosphorus on June 13 →				
3) Shoot density on June 19	+ 31.3% (*)	+ 26.3% NS	+ 16.4% NS	+ 76.9% NS	+ 21.9% NS
4) Shoot density on June 19 in percent of final shoot density	+ 13.1% NS	+ 12.8% NS	- 5.1% NS	+ 34.2% NS	+ 22.8% NS
5) Final shoot density	+ 14.2% NS	+ 5.5% NS	+ 21.2% NS	+ 15.8% NS	+ 15.1% NS
6) Shoot height on June 19	+ 9.9% NS	+ 2.8% NS	+ 16.2% NS	+ 2.2% NS	+ 33.8% NS
7) Final shoot height	+ 5.6% NS	+ 8.5% NS	+ 10.5% NS	+ 0.5% NS	+ 2.1% NS
8) Basal shoot circumference	+ 2.4% NS	+ 9.4% NS	+ 17.0% NS	- 10.5% NS	- 7.3% NS
9) Number of leaves per shoot	+ 3.0% NS	+ 0.7% NS	+ 12.5% NS	- 2.8% NS	+ 1.9% NS
10) Length of the assimilation period 0%	+ 1.5% NS	+ 1.6% NS	+ 6.6% *	- 1.9% NS	- 0.4% NS
11) Length of the assimilation period 50%	+ 0.2% NS	+ 0.5% NS	+ 3.4% NS	- 1.9% NS	- 1.8% NS
12) Start of the assimilation period 0%	← Start of AP 0% before phosphorus was added →				
13) Start of the assimilation period 50%	+ 1.0 days NS	+ 2.9 days NS	+ 1.0 days NS	- 0.6 days NS	+ 0.9 days NS
14) Day after May 15 on which shoot height reached 71.1 cm	- 0.6 days NS	+ 0.5 days NS	- 2.1 days NS	- 2.5 days NS	+ 1.5 days NS
15) Duration of senescence 50% (yellowing halfway through)	+ 1.4 days NS	+ 3.7 days NS	+ 4.5 days NS	- 2.2 days NS	- 0.6 days NS
16) Duration of senescence 100% (yellowing complete)	+ 1.6 days NS	+ 2.7 days NS	+ 9.5 days *	- 2.7 days NS	- 3.3 days NS
17) Green height in percent of total height on October 3	+ 0.4% NS	+ 7.5% NS	+ 14.3% NS	- 25.1% NS	- 9.5% NS
18) Susceptibility to drought (percent leaf die-back on June 19)	+290.0% ***	0.0% NS	0.0% NS	+ 36.4% NS	+330.4% ***
19) Insect damage (percent infested shoots)	- 16.5% NS	- 47.2% NS	+ 45.3% NS	0.0% NS	- 32.5% NS
20) Typha shoot standing crop on June 19	+ 37.9% (*)	+ 27.9% NS	+ 56.9% NS	+ 77.6% NS	- 6.9% NS
21) Typha shoot standing crop in Oct./Nov.	+ 23.7% NS	+ 35.7% NS	+ 39.0% NS	+ 16.8% NS	- 11.6% NS
22) Standing crop of plants other than Typha in Oct./Nov.	← no measurements →				
23) Litter load in Oct./Nov.	← no measurements →				

for the application of phosphorus, addition of lime accelerated shoot emergence under all draining x burning regimes. In contrast, liming did not significantly affect the susceptibility of Typha plants to drought. As was the case for the other fertilizer treatments, application of lime did not markedly influence the percentage on Typha shoots infested by stem-boring insect larvae. The litter load was not measured in limed plots. In conclusion, the response of Typha glauca to liming was not very marked but rather favourable. This is consistent with the general observation that liming improves the microbial activity and leads to largely increased plant growth only in acid soils with a pH less than 5.0-5.5 but not in soil of pH 6.0 or greater where, on the contrary, sometimes lime-induced growth depressions can be observed (HAYNES 1984). Such lime-induced growth depressions have been attributed to deficiencies of micronutrients and possibly phosphorus (HAYNES 1984). Since in the present experiment the pH of the water in the impoundment was 6.5 (near the mat surface 6.2-4.8; HOGG and WEIN 1988a), no major impact of liming on Typha growth was to be expected.

The finding that the application of 200 kg/ha nitrogen increased Typha glauca shoot standing crop 3.6 times more than addition of 200 kg/ha phosphorus (+86% vs. +24%) is consistent with the observation of BEAUCHAMPS and KEREKES (1980) that newly flooded impounded freshwater marshes in Atlantic Canada tend to be limited by nitrogen, phosphorus becoming limiting only in older impoundments. By contrast, BOYD and HESS (1970) reported for 28 natural Typha latifolia stands in the southeastern United States that environmental phosphorus levels accounted for about two thirds of the variation in standing crop and that environmental nitrogen levels were not correlated with Typha biomass. ADRIANO et al. (1980) as well as SHAVER and MELILLO (1984) found in growth-chamber

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Table 9 (page 98). The effect of fertilizing with **phosphorus** (200 kg/ha) on biometric characteristics of Typga glauca under four different draining x burning regimes. Values are differences to the unfertilized treatment. If differences are given in days, minus stands for earlier and plus for later.
Significance symbols (planned orthogonal comparisons):
(*) = P<0.06, * = P<0.05, ** = P<0.01, *** = P<0.001
NS = P>0.06

Parameter	Difference limed vs. unfertilized				
	All draining and burning treatments combined	Undrained treatments only		Drained treatments only	
		unburned	burned	unburned	burned
1) Start of shoot emergence	Start of emergence before lime was added				
2) Shoot density on June 12	Application of lime on June 13				
3) Shoot density on June 19	+ 23.8% NS	- 9.4% NS	+ 16.4% NS	+ 53.0% NS	+ 79.2% NS
4) Shoot density on June 19 in percent of final shoot density	+ 10.1% NS	- 11.8% NS	- 13.0% NS	+ 1.7% NS	+124.8% **
5) Final shoot density	+ 13.4% NS	+ 3.4% NS	+ 35.9% NS	+ 34.7% NS	- 17.6% NS
6) Shoot height on June 19	+ 5.4% NS	- 2.9% NS	+ 7.1% NS	+ 7.0% NS	+ 25.6% NS
7) Final shoot height	+ 2.3% NS	- 3.0% NS	+ 3.4% NS	+ 3.1% NS	+ 7.0% NS
8) Basal shoot circumference	- 4.0% NS	- 4.7% NS	+ 4.4% NS	- 9.9% NS	- 6.0% NS
9) Number of leaves per shoot	- 1.8% NS	- 0.8% NS	- 0.1% NS	- 3.3% NS	- 2.6% NS
10) Length of the assimilation period 0%	- 1.8% NS	- 2.8% NS	+ 2.1% NS	- 5.1% NS	- 1.6% NS
11) Length of the assimilation period 50%	- 1.3% NS	- 0.3% NS	+ 1.7% NS	- 2.0% NS	- 5.1% NS
12) Start of the assimilation period 0%	Start of AP 0% before lime was added				
13) Start of the assimilation period 50%	0.0 days NS	- 1.8 days NS	+ 1.6 days NS	- 0.2 days NS	+ 0.6 days NS
14) Day after May 15 on which shoot height reached 71.1 cm	- 0.4 days NS	- 0.4 days NS	+ 0.7 days NS	- 2.7 days NS	+ 0.7 days NS
15) Duration of senescence 50% (yellowing halfway through)	- 1.1 days NS	- 2.1 days NS	+ 3.3 days NS	- 1.9 days NS	- 3.9 days NS
16) Duration of senescence 100% (yellowing complete)	- 3.6 days (*)	- 4.6 days NS	+ 3.0 days NS	- 7.2 days *	- 5.6 days NS
17) Green height in percent of total height on October 3	- 16.1% NS	- 4.7% NS	+ 11.6% NS	- 53.3% NS	- 40.8% *
18) Susceptibility to drought (percent leaf die-back on June 19)	+ 40.0% NS	0.0% NS	0.0% NS	+154.5% NS	+ 21.7% NS
19) Insect damage (percent infested shoots)	+ 10.1% NS	+ 9.1% NS	+ 16.5% NS	0.0% NS	-100.0% NS
20) Typha shoot standing crop on June 19	+ 3.2% NS	- 18.9% NS	+ 24.9% NS	+ 98.8% NS	+ 55.2% NS
21) Typha shoot standing crop in Oct./Nov.	+ 22.0% NS	+ 20.0% NS	+ 38.0% NS	+ 46.3% NS	- 21.3% NS
22) Standing crop of plants other than Typha in Oct./Nov.	no measurements				
23) Litter load in Oct./Nov.	no measurements				

experiments that the biomass of T. latifolia was correlated to the supply of both phosphorus and nitrogen; however, in both studies phosphorus accounted again for more of the variance than nitrogen. ADRIANO et al. (1980) reported that the addition of 60 ppm phosphorus to the floodplain soil used as growing medium increased total standing crop by approximately 29% as compared to the 17% increase brought about by the application of 100 ppm nitrogen. SHAVER and MELILLO (1984) observed in their growth-chamber study with T. latifolia that a 9-fold increase in the weekly supply of phosphorus (from 0.006 to 0.055 g P per week and 7 liter pot) augmented the standing crop of the new shoots produced during the experiment by 70% whereas a 9-fold increase in the weekly supply of nitrogen (from 0.042 to 0.375 g N per week and 7 liter pot) enhanced the standing crop by only 48%. Another difference between the results of the present experiment and those of ADRIANO et al. (1980) and SHAVER and MELILLO (1984) became apparent when the increase in Typha shoot biomass brought about by the combined application of nitrogen and phosphorus (and lime in the present experiment) was compared with the increases brought about by the addition of only one of the two fertilizers. In the present experiment the increase in Typha shoot standing crop due to fertilizing with only nitrogen or phosphorus added up to 83% of the increase resulting from the combined application of nitrogen and phosphorus, as compared to 73% and 55% in the experiments of ADRIANO et al. (1980) and SHAVER and MELLILO (1984), respectively.
However, fertilizer experiments with the freshwater macrophyte Phragmites australis cultivated under controlled conditions (BORNKAMM and RAGHI-ATRI 1978, BORNKAMM et al. 1979, 1980, RAGHI-ATRI and BORNKAMM 1980) as well as fertilizer experiments in saltmarshes under natural conditions in the temperate (see e.g. VALIELA et al. 1982 for bibliography) and sub-arctic (e.g. CARGILL and JEFFERIES 1984) zone, showed that as in

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Table 10 (page 100). The effect of **liming** at a rate of 625 kg/ha on biometric characteristics of Typga glauca under four different draining x burning regimes. Values are differences to the unfertilized treatment. If differences are given in days, minus stands for earlier and plus for later.
Significance symbols (planned orthogonal comparisons):
(*) = P<0.06, * = P<0.05, ** = P<0.01, *** = P<0.001
NS = P>0.06

the present study growth was primarily limited by nitrogen and that phosphorus became limiting only when nitrogen was supplemented. In contrast to our findings with Typha glauca, however, BORNKAMM and RAGHI-ATRI (1978) and BORNKAMM et al. (1979) reported for Phragmites communis that fertilizing with nitrogen increased the percentage of shoots infested by insects.

5.4. CONCLUSIONS

The objective of the present study was to investigate the impacts of draining and burning on the nutrient status of Typha glauca floating mats in a water-level stabilized marsh and to compare them with the effect of fertilizing with known amounts of nitrogen, phosphorus and lime.

The fertilizer experiments revealed that Typha growth in the marsh studied was primarily limited by lack of nitrogen, since nitrogen enrichment resulted in a significant increase in yield but did practically not change species composition nor relative abundance (LEE et al. 1983). Burning, however, did unlike fertilizing with nitrogen alone or in combination with phosphorus and lime not increase Typha shoot standig crop, indicating that the amount of nitrogen released through the fire and made available to plants was not sufficient to stimulate growth. Draining, finally, resulted in a significantly reduced Typha shoot standing crop; apparently the more rapid mineralisation of organic soil matter due to improved soil aeration in the drained treatments did not compensate for the lower soil temperatures in the rooting zone of Typha which reduced the rate of nutrient uptake and, therefore, Typha growth.

It is concluded that burning did not markedly improve the nutrient cycling in the Typha ecosystem studied and did, consequently, not bring about the revitalization postulated by WEIN's (1983) paludification-fire-nutrient release hypothesis. This lack of improvement in the nutrient status was probably due to the low intensity of the fire that consumed only surface litter but did not penetrate into the organic soil. Likewise, in the marsh ecosystem studied draining did not result in the substantial release of nutrients and the revitalization observed in

North American prairie marshes during periods of drought (WELLER and SPATCHER 1965, WELLER 1978, 1982, VAN DER VALK and DAVIS 1978a,b, 1979, VAN DER VALK 1981).

SUMMARY

The effects of draining and spring burning on the nutrient status of Typha glauca floating mats in a water-level stabilized freshwater marsh were examined in Eastern Canada (New Brunswick) and compared to the impact of fertilizer applications.
Treatment effects were evaluated in terms of phenological and growth characteristics of Typha glauca, using Typha as a phytometer. The parameters measured were (1) shoot emergence, (2) final shoot density, (3) final shoot height, (4) basal shoot circumference, (5) number of leaves per shoot, (6) duration of the assimilation period, (7) senescence, (8) susceptibility to drought, (9) damage by stem-boring insect larvae, (10) shoot standing crop and (11) litter load.

Draining lowered the water table to about 30 cm below soil surface and reduced Typha shoot standing crop to 64% of that in the undrained treatments. Reduced growth is assumed to be caused primarily by lower mean temperatures in the rooting zone of Typha rather than by lack of water or poor availability of nutrients; low substrate temperatures reduce the rate of nutrient uptake. During extended drought periods, however, water can become temporarily limiting under drained conditions, and then particularly in burned and/or fertilized treatments.

Burning in spring affected most of the growth parameters measured but did not significantly change Typha shoot standing crop; the nutrients released and made available to plants through combustion of surface litter were insufficient in quantity to stimulate Typha growth.

Nitrogen was the primary growth limiting factor. Addition of 200 kg/ha actual nitrogen resulted in a significant 1.86-fold increase in Typha shoot standing crop.

Phosphorus was not ordinarily limiting but became limiting when nitrogen was supplemented. When no nitrogen was added, application of 200 kg/ha actual phosphorus resulted only in a 1.24-fold increase (not significant) in Typha shoot standing crop. Addition of the same amount of phosphorus in combination with nitrogen (200 kg/ha) and lime 625 kg/ha), on the other hand, resulted in a significant 2.31-fold increase in shoot standing crop.

Liming at a rate of 625 kg/ha did not significantly affect Typha shoot production.

It is concluded that neither draining nor burning improved the supply of limiting nutrients sufficiently to stimulate Typha growth. Typha shoot production was primarily limited by nitrogen and secondarily only by phosphorus, which became limiting when nitrogen was supplemented.

ZUSAMMENFASSUNG

In der vorliegenden Arbeit wurden die Auswirkungen von Drainage und kontrolliertem Abbrennen im Frühjahr auf die Nährstoffversorgung von schwimmenden *Typha glauca*-Beständen in einem eingedeichten Süsswasser-Feuchtgebiet in Ost-Kanada (New Brunswick) untersucht und mit der Wirkung von Düngergaben verglichen.
Zur Beurteilung der Auswirkungen der verschiedenen Bewirtschaftungsmassnahmen wurde *Typha* selbst als Indikatororganismus verwendet, wobei die folgenden phänologischen und biometrischen Grössen gemessen wurden: (1) Erscheinen der Halme, (2) Zahl der *Typha*-Halme pro Flächeneinheit, (3) Höhe der Halme, (4) Halmumfang am Boden, (5) Anzahl der Blätter pro Halm, (6) Dauer der Assimilationsperiode, (7) Absterben der Halme, (8) Trockenheitsanfälligkeit, (9) Insektenbefall, (10) Gewicht der *Typha*-Halme pro Flächeneinheit und (11) Gewicht der Streue pro Flächeneinheit.

Die **Drainage** senkte den Wasserspiegel auf ca. 30 cm unter die Bodenoberfläche und verminderte die oberirdische *Typha*-Biomasse auf 64% derjenigen in den nicht-drainierten Flächen. Der Produktionsausfall scheint weniger auf Wassermangel oder ungünstigere Nährstoffversorung in den drainierten Flächen zurückzugehen als vielmehr auf die kühleren Temperaturen im *Typha*-Wurzelbereich; niedrige Bodentemperaturen wirken sich nachgewiesenermassen ungünstig auf die Nährstoffaufnahme aus. Treten allerdings längere Tockenperioden auf, dann kann das Wasser in drainierten Flächen zum wachstumsbegrenzenden Faktor werden, vor allem in Flächen, die zusätzlich zur Drainage noch gebrannt oder gedüngt wurden.

Kontrolliertes Abbrennen im Frühjahr beeinflusste die Mehrzahl der gemessenen biometrischen Grössen, wirkte sich indessen nicht signifikant auf die oberirdische *Typha*-Biomasse aus. Die Menge der bei der Verbrennung der Streue freigesetzten Nährstoffe genügte offensichtlich nicht, um das Wachstum von *Typha glauca* zu stimulieren.

Stickstoff erwies sich als primärer limitierender Faktor. Gaben von 200 kg Stickstoff pro ha erhöhten die Masse der pro Flächeneinheit produzierten *Typha*-Halme um das 1.86-fache.

Phosphor war zwar normalerweise nicht limitierend, wurde es jedoch auf Stickstoff gedüngten Flächen. Wurde nur mit Phosphor gedüngt (200 kg P/ha), so ergab sich eine 1.24-fache, nicht signifikante Zunahme der oberirdischen *Typha*-Biomasse. Wurde hingegen die gleiche Menge Phosphor (200 kg/ha) zusammen mit ebensoviel Stickstoff (200 kg N/ha) und 625 kg Kalk pro ha zugegeben, so nahm die *Typha*-Biomasse pro Flächeneinheit signifikant auf das 2.31-fache zu.

Kalkgaben von 625 kg/ha zeitigten keine signifikante Wirkung auf die Biomasse der pro Flächeneinheit produzierten *Typha*-Halme.

Zusammengefasst ergibt sich als Schlussfolgerung, dass weder Drainage noch kontrolliertes Abbrennen im Frühjahr die Nährstoffversorgung in einem Masse verbesserten, das ausreichte, um das Wachstum von *Typha glauca* zu stimulieren. Es zeigte sich, dass in erster Linie mangelhafte Stickstoffversorgung die Biomasseproduktion von *Typha* begrenzte; Phosphor war erst in zweiter Linie limitierend, und dies nur auf mit Stickstoff gedüngten Flächen.

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APPENDICES

Legend to the appendices 1-23

Fertilizer treatments:
- C = no fertilizer added
- N = nitrogen added (200 kg/ha)
- P = phosphorus added (200 kg/ha)
- L = lime added (625 kg/ha)
- NPL = nitrogen, phosphorus and lime added at above rates

Significance testing:

Tested were the pairwise comparisons listed below: if two of the means compared share the same letter they are not significantly different at $P<0.05$. Compared were (see Table below):
- The two draining means (A) (all burning and fertilizer treatments combined; n = 50);
- the two burning means (B) (all draining and fertilizer treatments combined; n = 50);
- the two burning means within a single draining regime (C and D, respectively) (all fertilizer treatments combined; n = 25);
- any two fertilizer treatment means (E) (all draining and burning treatments combined; n = 20);
- any two fertilizer treatment means within a single draining treatment (F and G, respectively) (the two burning treatments combined; n = 10);
- any two fertilizer treatment means within a single burning treatment (H and I, respectively) (the two draining treatments combined; n = 10);
- any two fertilizer treatment means within a single draining x burning regime (K, L, M and N, respectively).

Sample sizes and pairwise comparisons tested. Numbers indicate the sample sizes on which means are based on, letters in parentheses the treatments for which pairwise comparisons were made. (For experimental design see Chapter 3.1)

Draining and burning treatments	Mean		Fertilizer treatments C		NPL		N		P		L	
Mean	100[1]		20	(E)	20	(E)	20	(E)	20	(E)	20	(E)
Undrained	50[2]	(A)	10	(F)	10	(F)	10	(F)	10	(F)	10	(F)
Drained	50[2]	(A)	10	(G)	10	(G)	10	(G)	10	(G)	10	(G)
Unburned	50[2]	(B)	10	(H)	10	(H)	10	(H)	10	(H)	10	(H)
Burned	50[2]	(B)	10	(I)	10	(I)	10	(I)	10	(I)	10	(I)
Undrained-unburned	25[3]	(C)	5	(K)	5	(K)	5	(K)	5	(K)	5	(K)
Undrained-burned	25[3]	(C)	5	(L)	5	(L)	5	(L)	5	(L)	5	(L)
Drained-unburned	25[3]	(D)	5	(M)	5	(M)	5	(M)	5	(M)	5	(M)
Drained-burned	25[3]	(D)	5	(N)	5	(N)	5	(N)	5	(N)	5	(N)

In appendices 39 and 40 the indices 1) = 40, 2) = 20, 3) = 10

Appendix 1. Start of shoot emergence (days after May 15)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	5.5	-	-	-	-	-
Undrained	0.0 a	-	-	-	-	-
Drained	11.0 b	-	-	-	-	-
Unburned	5.5	Shoot emergence started before burning and fertilizer treatments were applied				
Burned	-					
Undrained-unburned	0.0	-	-	-	-	-
Undrained-burned	-	-	-	-	-	-
Drained-unburned	11.0	-	-	-	-	-
Drained-burned	-	-	-	-	-	-

Appendix 2. Shoot density on June 12 (shoots per square meter)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	5.7	-	-	-	-	-
Undrained	8.2 a	-	-	-	-	-
Drained	3.2 b	-	-	-	-	-
Unburned	4.4 a	Fertilizer had not yet been applied by June 12				
Burned	7.0 b					
Undrained-unburned	7.4 a	-	-	-	-	-
Undrained-burned	9.0 a	-	-	-	-	-
Drained-unburned	1.4 a	-	-	-	-	-
Drained-burned	7.0 b	-	-	-	-	-

Appendix 3. Shoot density on June 19 (shoots per square meter)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	17.9	16.0 a	17.2 a	15.5 a	21.0 a	19.8 a
Undrained	21.3 a	21.3 a	19.6 a	17.6 a	25.8 a	22.1 a
Drained	14.5 b	10.7 a	14.8 a	13.4 a	16.2 a	17.6 a
Unburned	18.0 a	16.5 a	16.9 a	14.5 a	23.8 a	18.6 a
Burned	17.8 a	15.5 a	17.6 a	16.5 a	18.2 a	21.0 a
Undrained-unburned	20.2 a	21.3 a	19.3 a	14.5 a	26.9 a	19.3 a
Undrained-burned	22.3 a	21.3 a	20.0 a	20.7 a	24.8 a	24.8 a
Drained-unburned	15.8 a	11.7 a	14.5 a	14.5 a	20.7 a	17.9 a
Drained-burned	13.2 a	9.6 a	15.1 a	12.4 a	11.7 a	17.2 a

Appendix 4. Shoot density on June 19 in percent of final shoot density

Draining and burning treatments	Mean	C	NPL	N	P	L
Mean	63.9	63.3 a	57.5 a	57.4 a	71.6 a	69.7 a
Undrained	69.9 a	79.7 ab	58.6 b	59.0 b	82.5 a	69.8 ab
Drained	57.9 b	46.9 a	56.5 a	55.8 a	60.8 a	69.5 a
Unburned	67.2 a	67.0 a	59.3 a	64.8 a	81.7 a	63.0 a
Burned	60.7 a	59.6 a	55.8 a	50.0 a	61.5 a	76.4 a
Undrained-unburned	69.4 a	75.7 ab	57.9 b	61.1 ab	85.4 a	66.8 ab
Undrained-burned	70.4 a	83.8 a	59.2 a	56.9 a	79.5 a	72.9 a
Drained-unburned	65.0 a	58.2 a	60.7 a	68.6 a	78.1 a	59.2 a
Drained-burned	50.9 a	35.5 a	52.3 ab	43.0 ab	43.6 ab	79.8 b

Fertilizer treatments: C, NPL, N, P, L

Appendix 5. Final shoot density (shoots per square meter)

Draining and burning treatments	Mean	C	NPL	N	P	L
Mean	28.6	25.4 a	31.1 a	28.7 a	29.0 a	28.8 a
Undrained	31.3 a	27.4 a	34.8 a	31.0 a	31.0 a	32.6 a
Drained	25.8 a	23.3 a	27.4 a	26.4 a	27.0 a	25.1 a
Unburned	27.0 a	25.6 a	28.2 a	23.0 a	28.2 a	29.9 a
Burned	30.0 a	25.2 a	33.9 a	34.3 a	29.8 a	27.7 a
Undrained-unburned	29.6 a	29.0 a	33.7 a	24.6 a	30.6 a	30.0 a
Undrained-burned	33.1 a	25.9 a	35.8 a	37.3 a	31.4 a	35.2 a
Drained-unburned	24.4 a	22.2 a	22.7 a	21.5 a	25.7 a	29.9 a
Drained-burned	27.3 a	24.5 a	32.1 a	31.3 a	28.2 a	20.2 a

Fertilizer treatments: C, NPL, N, P, L

Appendix 6. Shoot height on June 19 (cm)

Draining and burning treatments	Mean	C	NPL	N	P	L
Mean	44.3	42.4 a	42.4 a	45.2 a	46.6 a	44.7 a
Undrained	57.7 a	56.7 a	55.7 a	57.2 a	61.4 a	57.4 a
Drained	30.8 b	28.2 a	29.1 a	33.2 a	31.9 a	32.0 a
Unburned	53.1 a	52.6 a	52.4 a	53.7 a	54.0 a	53.0 a
Burned	35.4 b	32.3 a	32.4 a	36.7 a	39.3 a	36.4 a
Undrained-unburned	68.1 a	68.4 a	68.0 a	67.2 a	70.3 a	66.4 a
Undrained-burned	47.3 b	45.1 a	43.4 a	47.2 a	52.4 a	48.3 a
Drained-unburned	38.2 a	36.9 a	36.8 a	40.2 a	37.7 a	39.5 a
Drained-burned	23.5 b	19.5 a	21.3 a	26.1 a	26.1 a	24.5 a

Fertilizer treatments: C, NPL, N, P, L

Appendix 7. Final shoot height (cm)

Draining and burning treatments	Mean	C	NPL	N	P	L
Mean	140.1	126.9 a	161.1 b	148.6 b	134.0 a	129.8 a
Undrained	147.0 a	135.3 a	163.1 b	152.9 ab	148.2 ab	135.4 a
Drained	133.2 b	118.5 a	159.2 c	144.2 bc	119.9 a	124.2 ab
Unburned	146.4 a	134.8 a	162.5 b	159.1 b	141.2 ab	134.7 a
Burned	133.8 a	119.0 a	159.8 b	138.0 a	126.9 a	125.0 a
Undrained-unburned	151.4 a	142.2 a	160.9 a	161.7 a	154.3 a	137.9 a
Undrained-burned	142.6 a	128.5 a	165.3 b	144.1 ab	142.0 ab	132.9 a
Drained-unburned	141.5 a	127.4 a	164.0 b	156.5 ab	128.0 a	131.4 a
Drained-burned	125.0 a	109.5 a	154.4 b	131.9 ab	111.8 a	117.2 a

Appendix 8. Basal shoot circumference (mm)

Draining and burning treatments	Mean	C	NPL	N	P	L
Mean	62.9	54.6 a	77.9 b	73.7 b	55.9 a	52.4 a
Undrained	65.6 a	56.1 a	77.8 c	74.7 cb	63.3 ab	55.9 a
Drained	60.3 b	53.2 a	78.1 b	72.7 b	48.5 a	49.0 a
Unburned	64.9 a	57.0 a	76.7 b	80.8 b	57.0 a	53.0 a
Burned	61.0 a	52.2 a	79.2 c	66.7 b	54.8 a	51.9 a
Undrained-unburned	67.4 a	59.8 ab	74.9 bc	80.0 c	65.4 abc	57.0 a
Undrained-burned	63.7 a	52.4 a	80.7 c	69.5 bc	61.3 abc	54.7 ab
Drained-unburned	62.4 a	54.3 a	78.4 b	81.6 b	48.6 a	48.9 a
Drained-burned	58.1 a	52.1 a	77.7 b	63.1 ab	48.3 a	49.0 a

Appendix 9. Number of leaves per shoot

Draining and burning treatments	Mean	C	NPL	N	P	L
Mean	8.39	7.74 a	9.63 b	9.02 b	7.97 a	7.60 a
Undrained	8.42 a	7.84 a	9.31 b	8.81 ab	8.33 ab	7.80 a
Drained	8.37 a	7.63 a	9.95 b	9.24 b	7.60 a	7.40 a
Unburned	8.49 a	7.89 a	9.33 b	9.66 b	7.82 a	7.73 a
Burned	8.30 a	7.58 a	9.93 b	8.39 a	8.12 a	7.48 a
Undrained-unburned	8.71 a	8.24 a	9.33 a	9.49 a	8.30 a	8.17 a
Undrained-burned	8.13 a	7.44 a	9.28 b	8.13 ab	8.37 ab	7.43 a
Drained-unburned	8.26 a	7.54 a	9.33 b	9.84 b	7.33 a	7.29 a
Drained-burned	8.47 a	7.72 a	10.59 b	8.65 a	7.87 a	7.52 a

Appendix 10. Length of the assimilation period 0% (days)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	149.8	146.6 a	154.2 b	155.2 b	148.8 ab	143.9 a
Undrained	160.5 a	155.2 a	165.2 b	166.6 b	161.2 ab	154.3 a
Drained	139.0 b	138.1 ab	143.3 ab	143.9 b	136.5 ab	133.4 a
Unburned	155.2 a	153.6 ab	160.9 b	160.6 b	153.5 ab	147.7 a
Burned	144.3 b	139.7 a	147.6 ab	149.9 b	144.2 ab	140.1 a
Undrained-unburned	169.0 a	165.8 ab	173.7 b	176.0 b	168.4 ab	161.2 a
Undrained-burned	152.0 b	144.5 a	156.7 ab	157.1 b	154.0 ab	147.5 ab
Drained-unburned	141.5 a	141.3 a	148.0 a	145.2 a	138.6 a	134.1 a
Drained-burned	136.6 a	134.9 a	138.5 a	142.6 a	134.3 a	132.8 a

Appendix 11. Length of the assimilation period 50% (days)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	97.3	95.6 a	97.7 a	103.1 b	95.8 a	94.4 a
Undrained	108.5 a	105.5 a	108.0 a	115.0 b	107.6 a	106.2 a
Drained	86.2 b	85.6 ab	87.5 ab	91.2 b	84.1 a	82.6 a
Unburned	99.3 a	98.1 ab	100.0 ab	103.7 b	97.6 ab	97.1 a
Burned	95.3 b	93.0 a	95.5 a	102.5 b	94.0 a	91.7 a
Undrained-unburned	112.0 a	110.5 a	111.9 a	116.2 a	111.1 a	110.2 a
Undrained-burned	105.0 b	100.6 a	104.1 a	113.8 b	104.0 a	102.3 a
Drained-unburned	86.7 a	85.8 a	88.1 a	91.2 a	84.2 a	84.1 a
Drained-burned	85.7 a	85.5 ab	86.9 ab	91.2 b	84.0 ab	81.1 a

Appendix 12. Start of the assimilation period 0% (days after May 15)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	12.9	-	-	-	-	-
Undrained	9.5 a	-	-	-	-	-
Drained	16.3 b	-	-	-	-	-
		Assimilation period 0% started before fertilizers were applied				
Unburned	5.5 a					
Burned	20.3 b					
Undrained-unburned	0.0 a	-	-	-	-	-
Undrained-burned	19.0 b	-	-	-	-	-
Drained-unburned	11.0 a	-	-	-	-	-
Drained-burned	21.5 b	-	-	-	-	-

Appendix 13. Start of the assimilation period 50% (days after May 15)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	47.5	46.1 a	51.1 b	47.1 a	47.1 a	46.1 a
Undrained	42.6 a	41.1 a	46.3 a	41.4 a	43.1 a	41.1 a
Drained	52.4 b	51.0 ab	55.9 b	52.8 a	51.1 ab	51.2 ab
Unburned	43.7 a	42.4 ab	46.5 b	44.8 ab	43.6 ab	41.4 a
Burned	51.3 b	49.7 ab	55.6 b	49.4 a	50.7 ab	50.9 ab
Undrained-unburned	38.1 a	36.9 a	39.8 a	39.0 a	39.8 a	35.1 a
Undrained-burned	47.1 b	45.4 ab	52.9 b	43.7 a	46.4 ab	47.0 ab
Drained-unburned	49.4 a	47.9 a	53.3 a	50.6 a	47.3 a	47.7 a
Drained-burned	55.4 b	54.1 a	58.4 a	55.1 a	55.0 a	54.7 a

Appendix 14. Day after May 15 on which shoot height reached 71.1 cm

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	48.8	50.5 a	47.4 a	46.4 b	49.9 a	50.1 a
Undrained	41.8 a	42.8 a	42.0 a	39.2 a	42.0 a	43.0 a
Drained	55.9 b	58.2 a	52.8 a	53.6 a	57.7 a	57.1 a
Unburned	43.4 a	45.0 a	43.1 a	41.6 a	44.0 a	43.4 a
Burned	54.3 b	56.0 a	51.7 a	51.3 a	55.7 a	56.7 a
Undrained-unburned	36.4 a	36.7 a	36.6 a	35.1 a	37.2 a	36.3 a
Undrained-burned	47.2 b	48.9 a	47.4 a	43.3 a	46.8 a	49.6 a
Drained-unburned	50.4 a	53.2 a	49.5 a	48.1 a	50.7 a	50.5 a
Drained-burned	61.3 b	63.1 a	56.0 a	59.2 a	64.6 a	63.8 a

Appendix 15. Duration of senescence 50% (day after the onset of senescence, i.e. Aug. 14, on which yellowing was halfway through)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	53.8	50.6 a	57.8 b	59.2 b	52.0 a	49.5 a
Undrained	60.1 a	55.7 a	63.3 ab	65.4 b	59.7 ab	56.3 a
Drained	47.6 b	45.6 a	52.4 b	53.0 b	44.2 a	42.8 a
Unburned	52.1 a	49.5 ac	55.5 bc	57.5 b	50.2 abc	47.5 a
Burned	55.6 b	51.8 a	60.2 b	60.9 b	53.7 a	51.5 a
Undrained-unburned	59.1 a	56.3 ab	60.6 ab	64.3 b	60.0 ab	54.2 a
Undrained-burned	61.1 a	55.0 a	66.0 ab	66.6 b	59.5 ab	58.3 ab
Drained-unburned	45.0 a	42.7 ab	50.4 b	50.8 b	40.5 a	40.8 a
Drained-burned	50.2 b	48.6 ab	54.3 b	55.3 b	48.0 ab	44.7 a

Appendix 16. Duration of senescence 100% (day after the onset of senescence, i.e. Aug. 14, on which yellowing was complete)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	71.6	69.0 a	76.3 b	76.9 b	70.6 a	65.4 a
Undrained	79.0 a	73.7 a	83.7 b	85.1 b	79.7 ab	72.8 a
Drained	64.3 b	64.4 ab	68.9 b	68.7 b	61.4 a	58.0 a
Unburned	69.7 a	68.1 a	75.4 b	75.1 b	68.0 a	62.2 a
Burned	73.5 b	70.0 ab	77.2 bc	78.4 c	73.1 abc	68.7 a
Undrained-unburned	78.0 a	74.8 ab	82.7 b	85.0 b	77.5 ab	70.2 a
Undrained-burned	80.0 a	72.5 a	84.7 b	85.1 b	82.0 ab	75.5 ab
Drained-unburned	61.5 a	61.3 ab	68.0 b	65.2 b	58.6 ab	54.1 a
Drained-burned	67.1 a	67.5 ab	69.7 ab	72.3 b	64.2 ab	61.9 a

Appendix 17. Green height in percent of total height on Oct. 3

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	58.3	53.9 a	69.7 b	68.4 b	54.1 a	45.2 a
Undrained	72.6 a	65.4 a	80.8 a	76.8 a	72.5 a	67.4 a
Drained	44.0 b	42.4 ab	58.7 b	60.0 b	35.8 a	23.0 a
Unburned	53.4 a	50.0 ab	63.9 b	64.5 b	48.5 ab	39.9 a
Burned	63.2 b	57.7 ac	75.6 b	72.2 bc	59.7 ac	50.6 a
Undrained-unburned	71.1 a	67.8 a	75.7 a	74.7 a	72.9 a	64.6 a
Undrained-burned	74.0 a	63.0 a	85.8 a	78.9 a	72.0 a	70.3 a
Drained-unburned	35.6 a	32.3 abc	52.1 bc	54.3 c	24.2 ab	15.1 a
Drained-burned	52.3 a	52.4 ab	65.3 b	65.6 b	47.4 ab	31.0 a

Appendix 18. Susceptibility to drought (percent leaf die-back on June 19)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	4.6 a	2.0 a	6.8 b	3.8 ab	7.8 b	2.8 ab
Undrained	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a
Drained	9.2 b	5.6 a	13.6 b	7.3 ab	15.6 b	5.6 ab
Unburned	1.4 a	0.5 a	3.6 a	0.9 a	0.7 a	1.4 a
Burned	7.8 b	3.4 a	10.0 bc	6.4 ab	14.8 c	4.2 ab
Undrained-unburned	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a
Undrained-burned	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a
Drained-unburned	2.9 a	1.1 a	7.3 a	1.8 a	1.5 a	2.8 a
Drained-burned	15.6 a	6.9 a	19.9 bc	12.8 ab	29.7 c	8.4 ab

Appendix 19. Insect damage (percent infested shoots)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	10.57	10.49 a	10.93 a	11.12 a	8.76 a	11.55 a
Undrained	20.34 a	20.14 a	19.86 a	21.65 a	17.51 a	22.53 a
Drained	0.80 b	0.83 a	2.00 a	0.59 a	0.00 a	0.56 a
Unburned	12.57 a	12.70 a	15.46 a	14.11 a	6.70 a	13.86 a
Burned	8.57 b	8.27 a	6.40 a	8.13 a	10.81 a	9.23 a
Undrained-unburned	24.10 a	25.40 a	26.92 a	27.04 a	13.40 a	27.72 a
Undrained-burned	16.58 b	14.88 a	12.80 a	16.26 a	21.62 a	17.34 a
Drained-unburned	1.04 a	0.00 a	4.00 a	1.18 a	0.00 a	0.00 a
Drained-burned	0.56 a	1.66 a	0.00 a	0.00 a	1.12 a	0.00 a

Appendix 20. Typha shoot standing crop on June 19 (g dry wt/m^2)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	26.1	24.8 a	24.1 a	21.5 a	34.2 a	25.6 a
Undrained	43.5 a	44.0 a	39.3 a	34.3 a	59.5 a	40.6 a
Drained	8.6 b	5.7 a	8.8 a	8.8 a	8.9 a	10.7 a
Unburned	37.2 a	37.0 a	35.6 a	29.2 a	49.4 a	35.0 a
Burned	14.9 b	12.7 a	12.6 a	13.9 a	19.0 a	16.3 a
Undrained-unburned	60.9 a	65.5 a	57.6 a	44.8 a	83.8 a	53.1 a
Undrained-burned	26.1 b	22.5 a	21.0 a	23.8 a	35.3 a	28.1 a
Drained-unburned	13.5 a	8.5 a	13.5 a	13.6 a	15.1 a	16.9 a
Drained-burned	3.7 b	2.9 a	4.2 a	4.0 a	2.7 a	4.5 a

Appendix 21. Typha shoot standing crop in Oct./Nov. (g dry wt/m^2)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	527.4	345.7 a	800.1 b	642.0 b	427.5 a	421.8 a
Undrained	644.6 a	422.7 a	945.1 b	731.6 ab	580.2 ab	543.3 a
Drained	410.2 b	268.7 a	655.1 b	552.3 b	274.8 a	300.3 a
Unburned	548.3 a	353.3 a	839.2 b	636.2 ab	454.6 a	458.5 a
Burned	506.5 a	338.1 a	761.0 b	647.8 b	400.3 a	385.2 a
Undrained-unburned	650.7 a	443.9 a	1005.4 b	669.4 ab	602.4 ab	532.6 a
Undrained-burned	638.4 a	401.4 a	884.9 b	793.9 ab	557.9 ab	554.0 ab
Drained-unburned	445.9 a	262.6 a	673.0 c	603.1 bc	306.8 ab	384.3 ab
Drained-burned	374.5 a	274.7 ab	637.2 c	501.6 bc	242.8 a	216.3 a

Appendix 22. Standing crop of plants other than *Typha* in Oct./Nov. (g dry wt/m^2)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	30.0	24.2 a	35.8 a	-	-	-
Undrained	50.0 a	43.2 a	56.8 b	-	-	-
Drained	10.0 b	5.2 a	14.8 a	-	-	-
Unburned	49.4 a	41.6 a	57.2 a	No measurements		
Burned	10.6 b	6.8 a	14.4 a			
Undrained-unburned	93.2 a	72.8 a	113.6 a	-	-	-
Undrained-burned	6.8 b	13.6 a	0.0 b	-	-	-
Drained-unburned	5.6 a	10.4 a	0.8 a	-	-	-
Drained-burned	14.4 a	0.0 a	28.8 b	-	-	-

Appendix 23. Litter load in Oct./Nov. (g dry wt/m^2)

Draining and burning treatments	Mean	Fertilizer treatments C	NPL	N	P	L
Mean	427.7	399.4 a	456.0 a	-	-	-
Undrained	415.4 a	429.6 a	404.8 a	-	-	-
Drained	436.0 a	369.1 a	507.2 a	-	-	-
Unburned	684.9 a	601.2 a	768.6 a	No measurements		
Burned	170.6 b	197.6 a	143.5 a			
Undrained-unburned	603.6 a	569.3 a	637.9 a	-	-	-
Undrained-burned	230.8 b	290.0 a	171.6 b	-	-	-
Drained-unburned	766.1 a	633.0 a	899.2 a	-	-	-
Drained-burned	110.3 b	105.2 a	115.4 a	-	-	-