Zeitschrift: Veröffentlichungen des Geobotanischen Institutes der Eidg. Tech. Hochschule, Stiftung Rübel, in Zürich

Herausgeber: Geobotanisches Institut, Stiftung Rübel (Zürich)

Band: 94 (1989)

Artikel: The impact of draining, burning and fertilizer treatments on the nutrient status of floating "Typha" mats in a freshwater marsh = Der Einfluss der Drainage, kontrolliertem Abbrennen und Düngung auf die Nährstoffverhältnisse in schwimmenden "Typha"-Beständen

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Kapitel: 4: Results

DOI: https://doi.org/10.5169/seals-308910

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

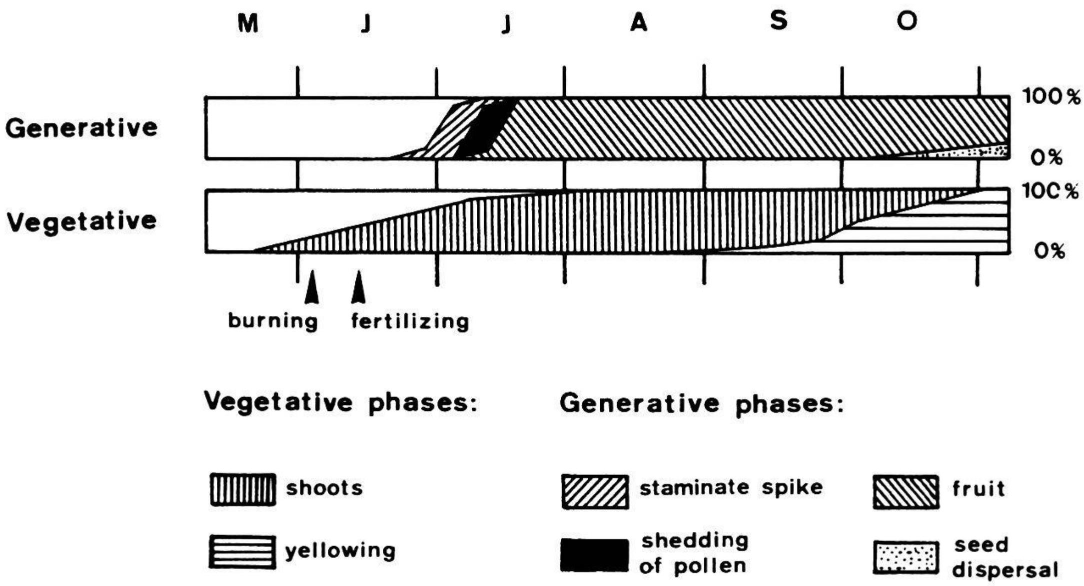


Fig. 8. General phenological development of *Typha glauca* during 1982 on unburned and unfertilized plots in the undrained basin.

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	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	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

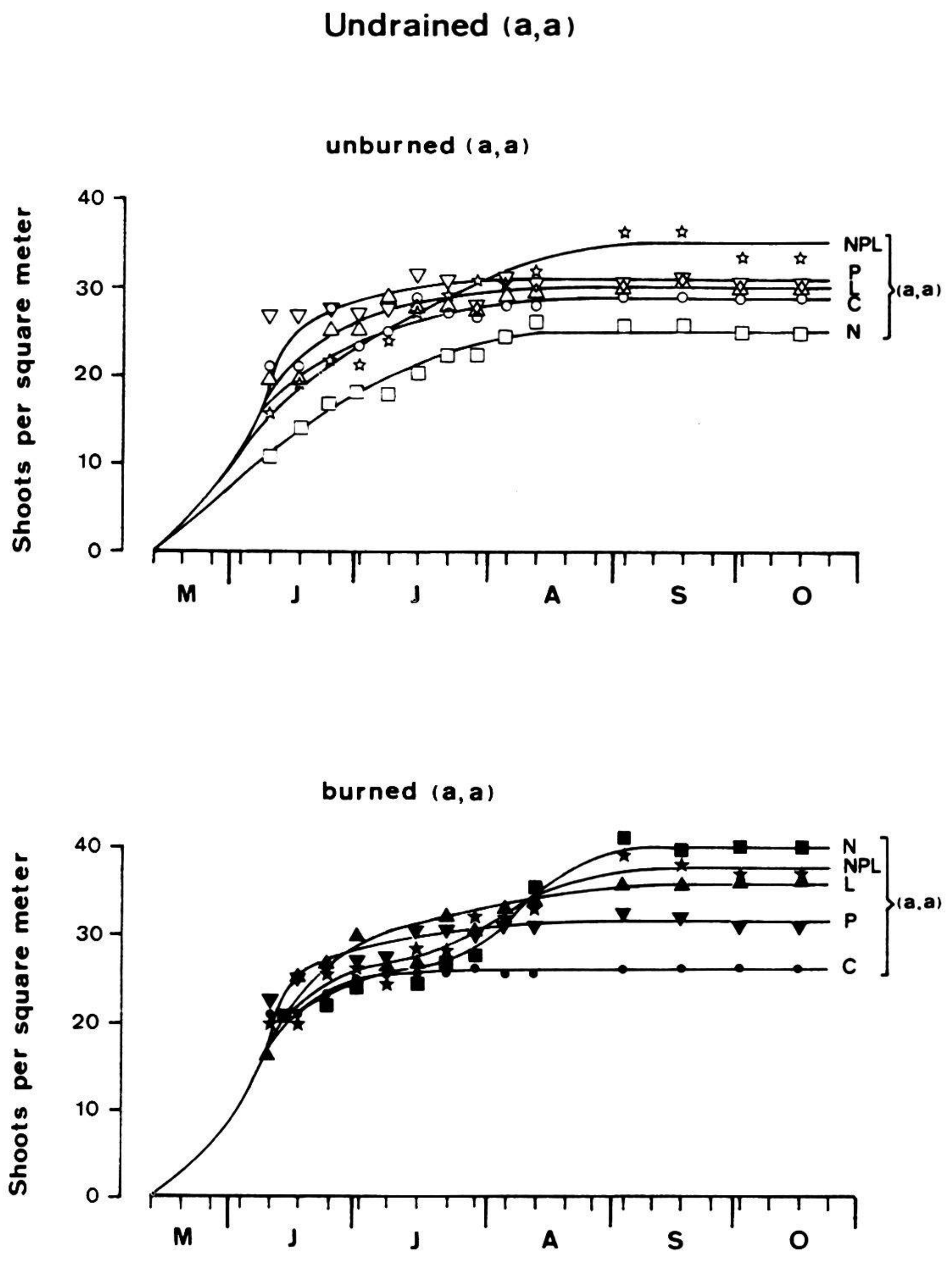


Fig. 9. Development of the shoot density (shoots per square meter) of Typha glauca in unburned (top) and burned (bottom) plots of the undrained basin, on which were superimposed five fertilizer treatments.
C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; 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.

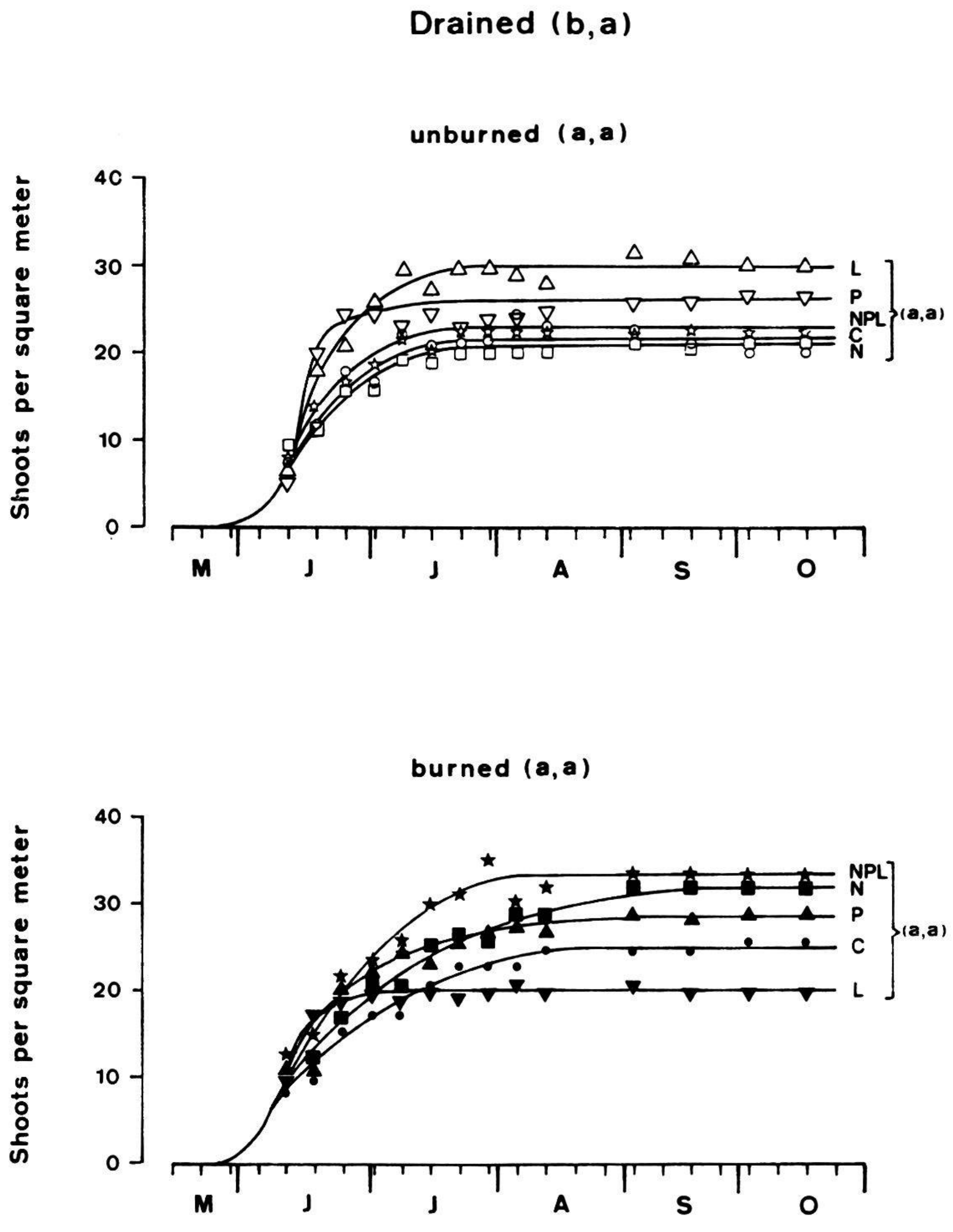


Fig. 10. Development of the shoot density (shoots per square meter) of Typha clauca in unburned (top) and burned (bottom) plots of the drained basin, on which were superimposed five fertilizer treatments.
C: unfertilized; NPL: nitrogen, phorphorus and lime added; N: nitrogen added; P: phosphorus added; 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.

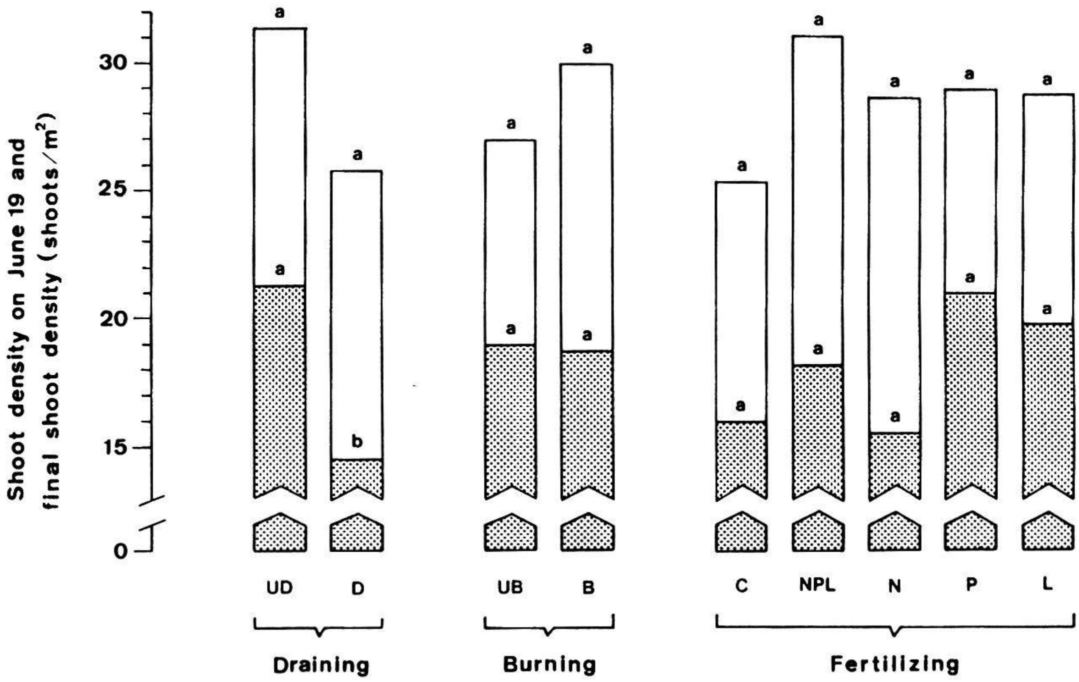


Fig. 11. Shoot density per square meter on June 19 (shaded portion) and final shoot density (entire bars) of Typha glauca under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** 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-

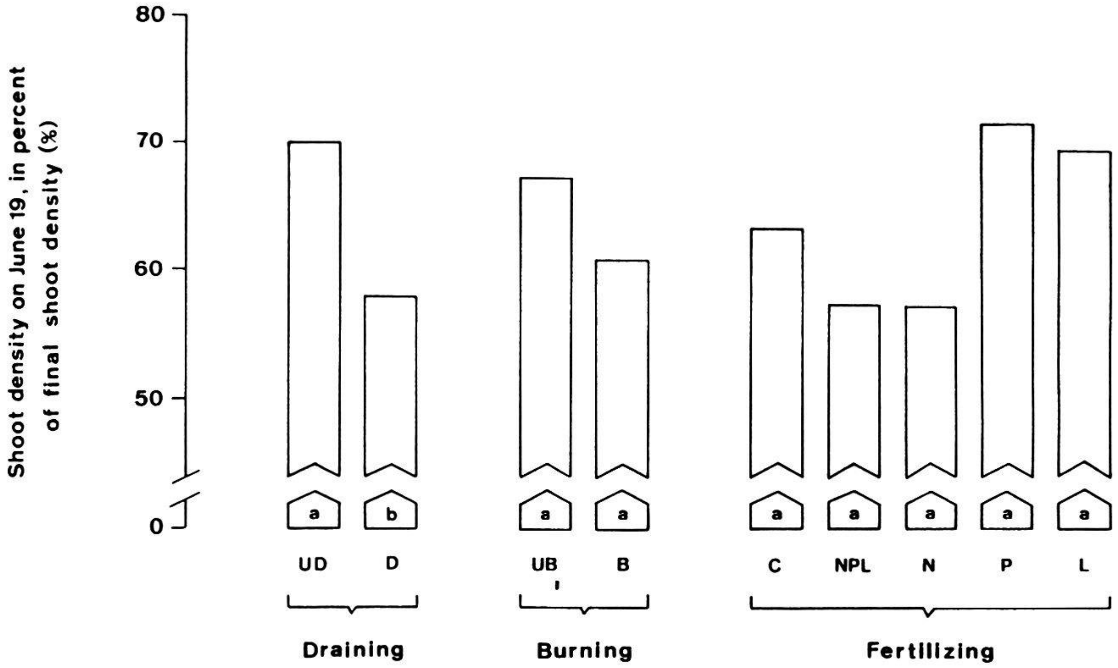


Fig. 12. Shoot density of <u>Typha glauca</u> on June 19, in percent of final density, under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; 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).

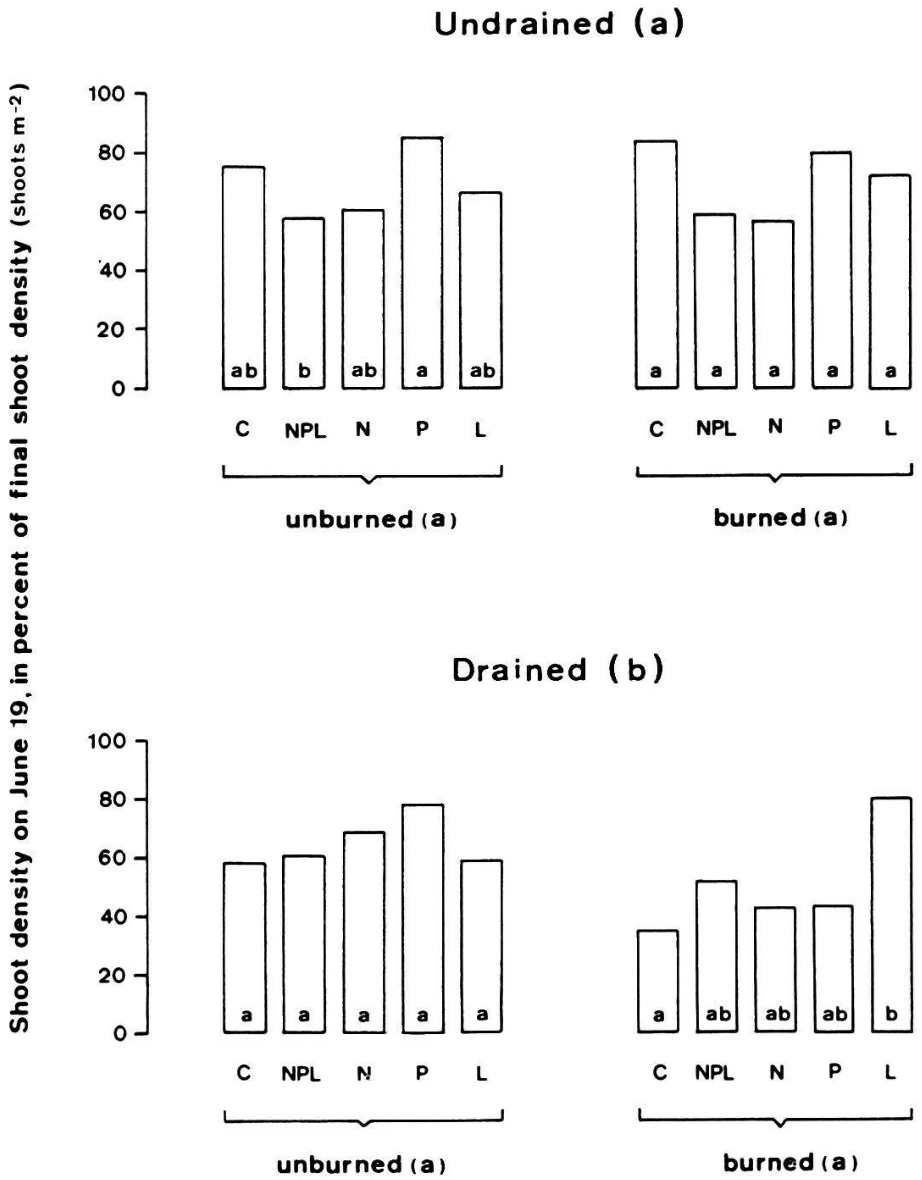


Fig. 13. Shoot density of Typha glauca on June 19, in percent of final density, in response to different fertilizer treatments which were superimposed on four draining x burning regimes. **Fertilizer treatments:** C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus 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

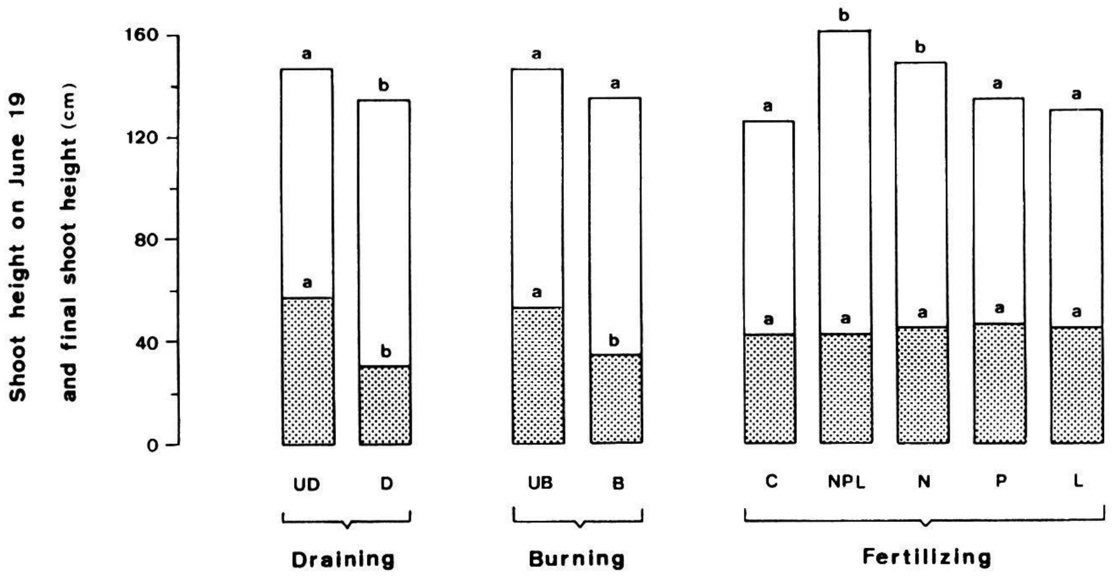


Fig. 14. Shoot height on June 19 (shaded portion) and final shoot height (entire bars) of Typha glauca under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; 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).

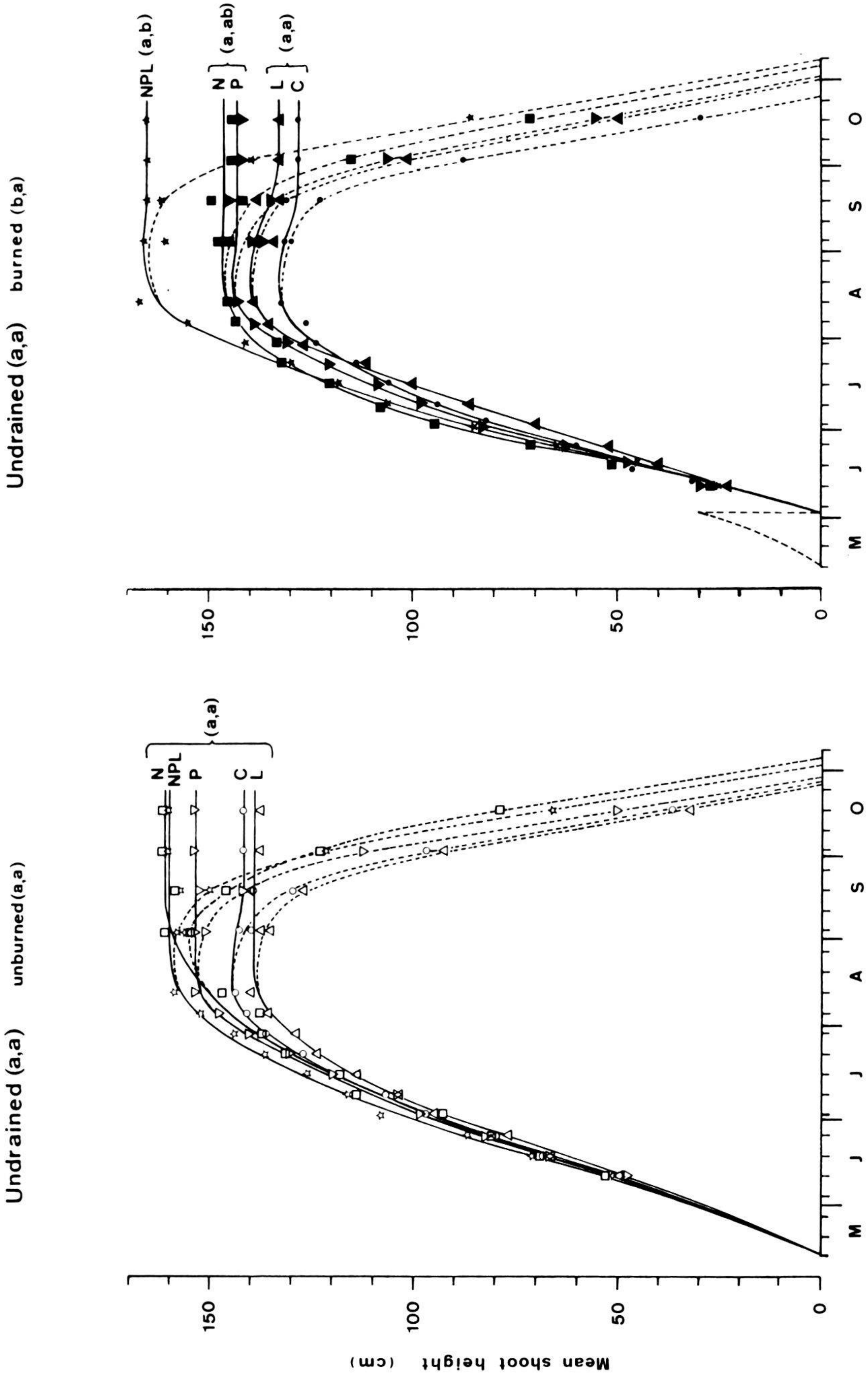

Undrained (a,a) unburned (a,a)
Undrained (a,a) burned (b,a)
N
NPL
P
C
L
(a,a)
NPL (a,b)
N
P
(a,ab)
L
C
(a,a)
Mean shoot height (cm)
150
100
50
0
M
J
J
A
S
O

Fig. 15.

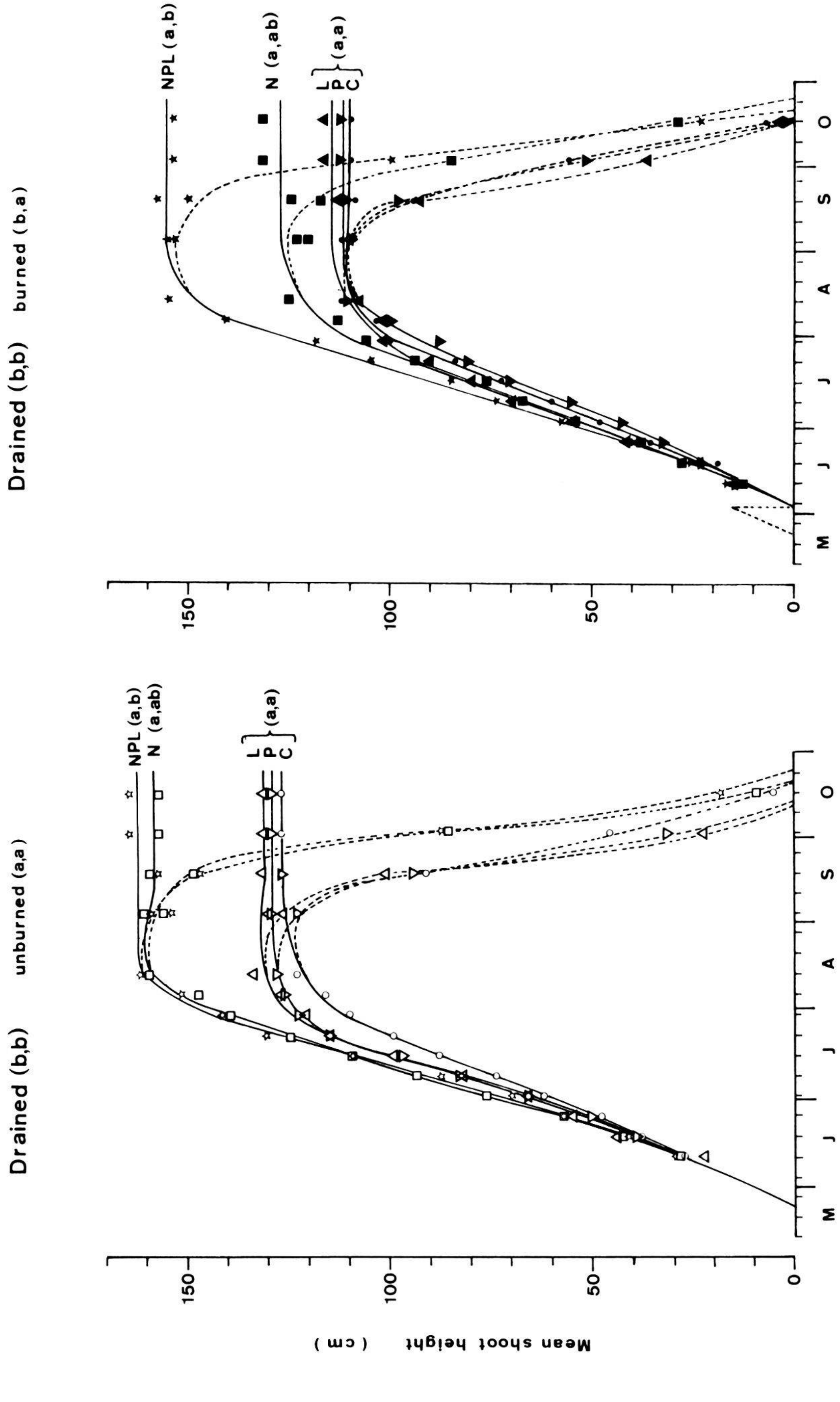

Drained (b,b) unburned (a,a)
Drained (b,b) burned (b,a)
NPL (a,b)
N (a,ab)
L
P
C
(a,a)
Mean shoot height (cm)
0
50
100
150
M
J
J
A
S
O

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.).

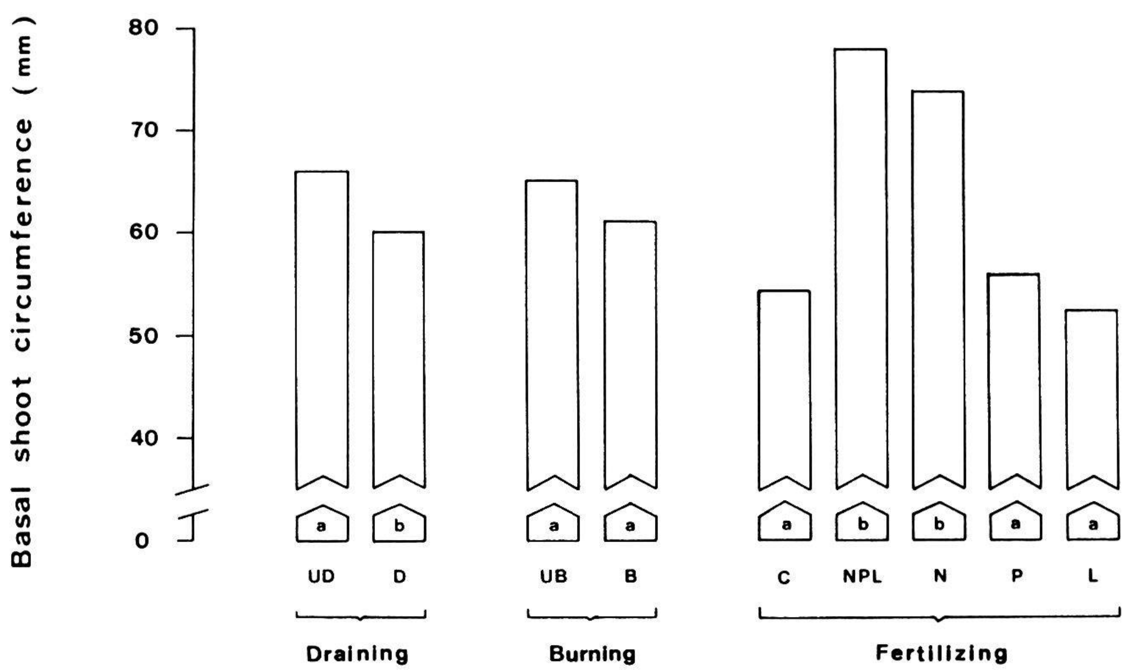


Fig. 17. Basal shoot circumference of <u>Typha glauca</u> under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer 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).

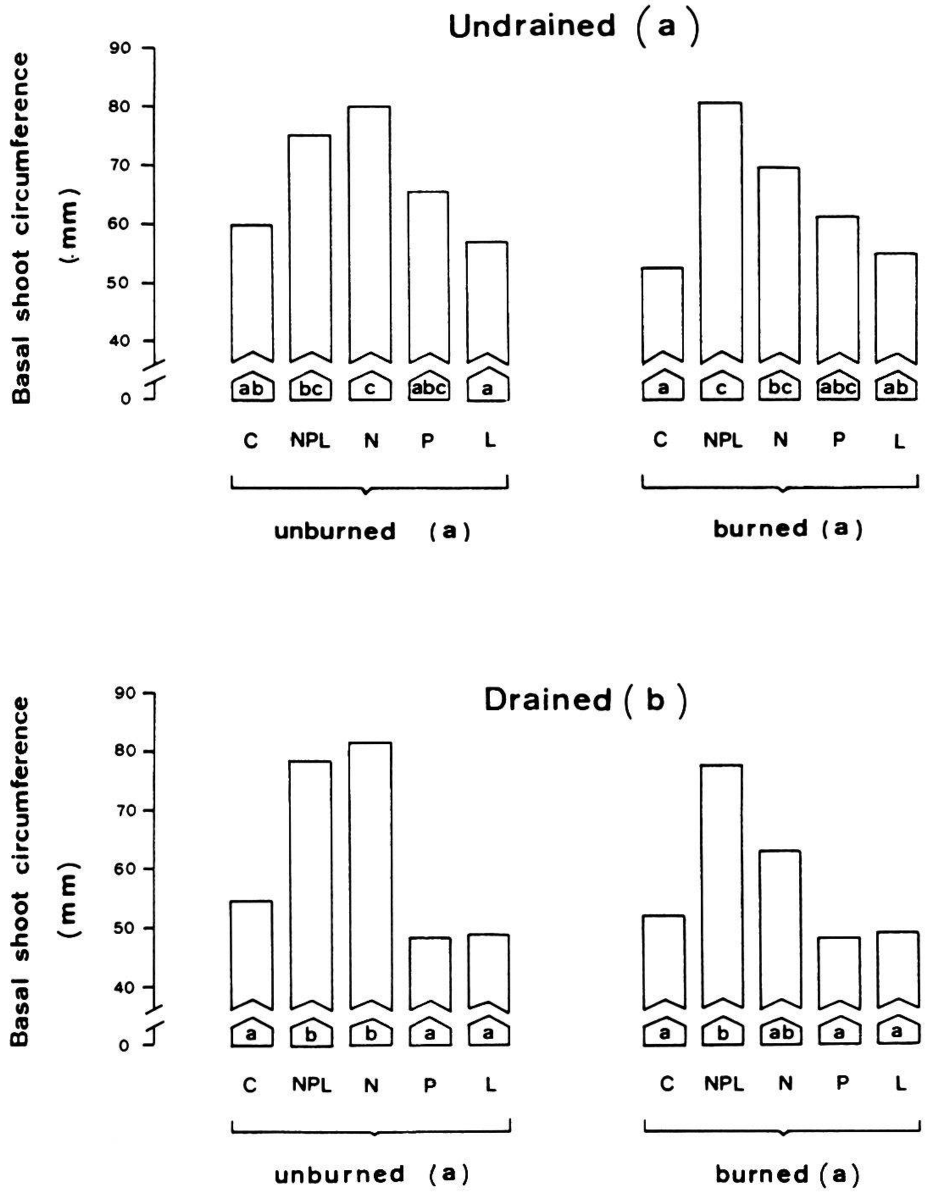


Fig. 18. Basal shoot circumference of <u>Typha glauca</u> in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; 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

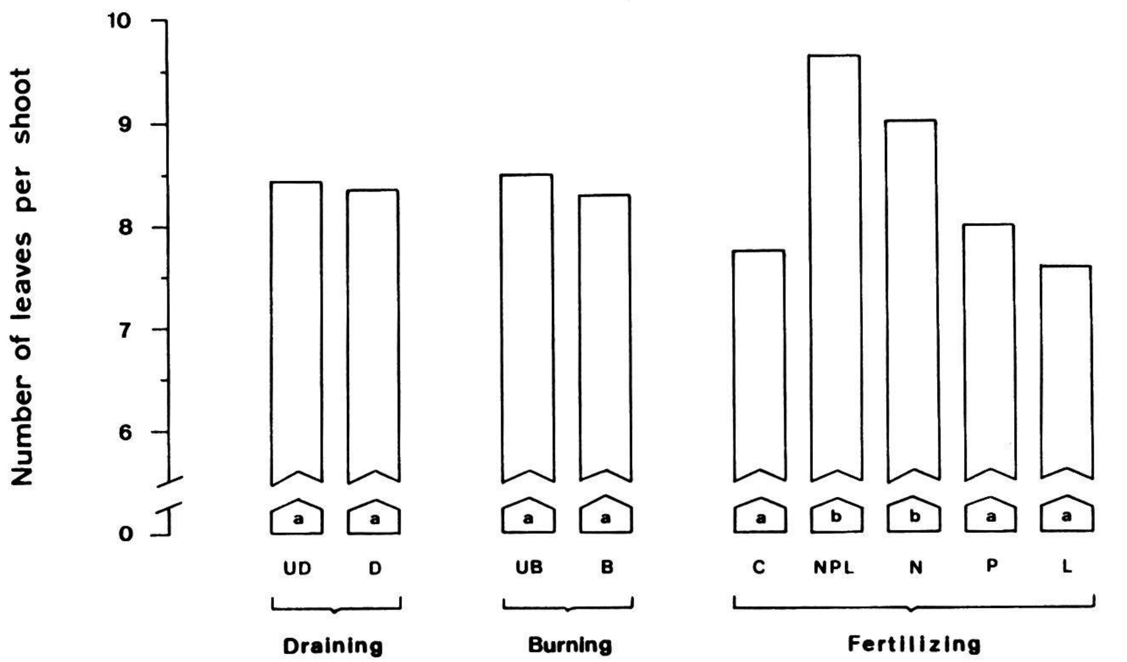


Fig. 19. Number of leaves per shoot of Typha glauca under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining and fertilizer 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).

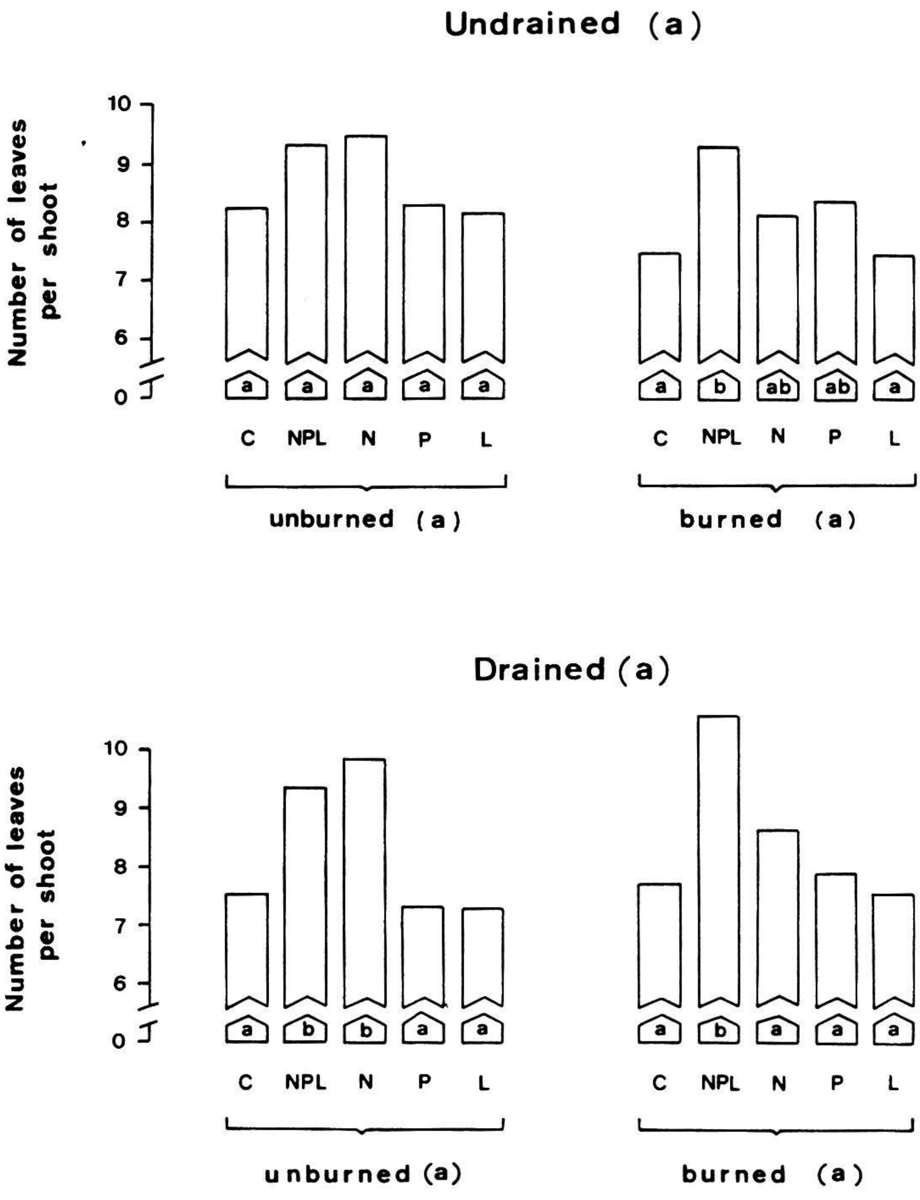


Fig. 20. Number of leaves per shoot of <u>Typha glauca</u> in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime added; 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).

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

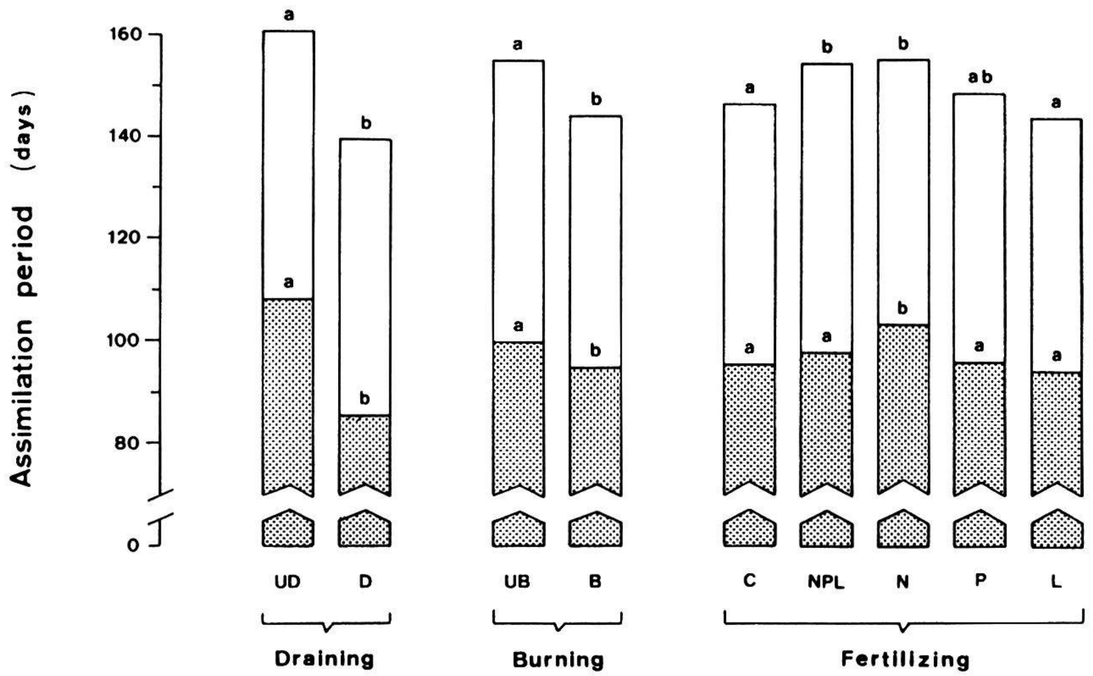


Fig. 21. Length of the assimilation periods 50% (AP 50%, shaded portion) and 0% (AP 0%, entire bars) of Typha glauca under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** 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).

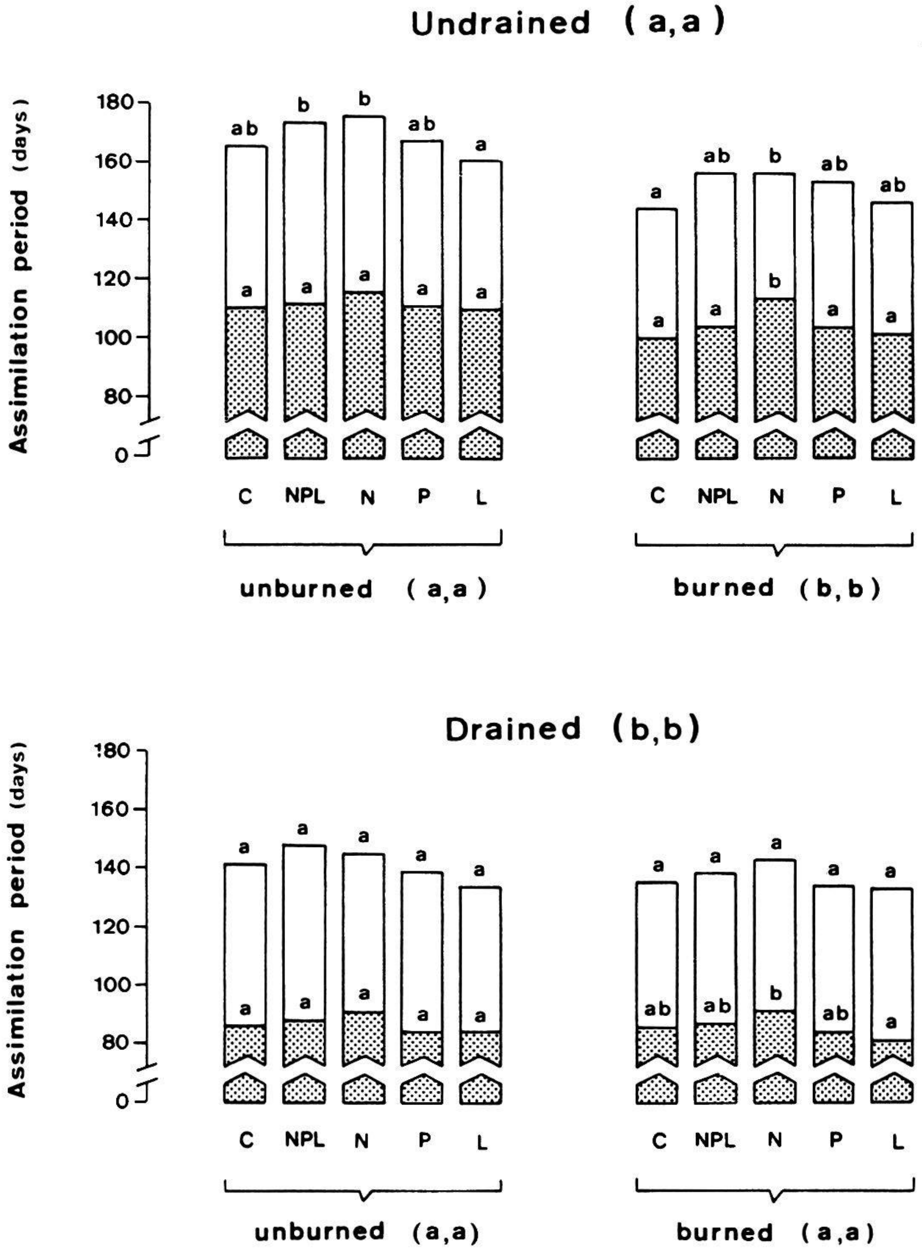


Fig. 22. Length of the assimilation periods 50% (AP 50%, shaded portion) and 0% (AP 0%; entire bars) of Typha glauca in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Values are means n = 5. Two draining treatment means (all burning and fertilizer 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.

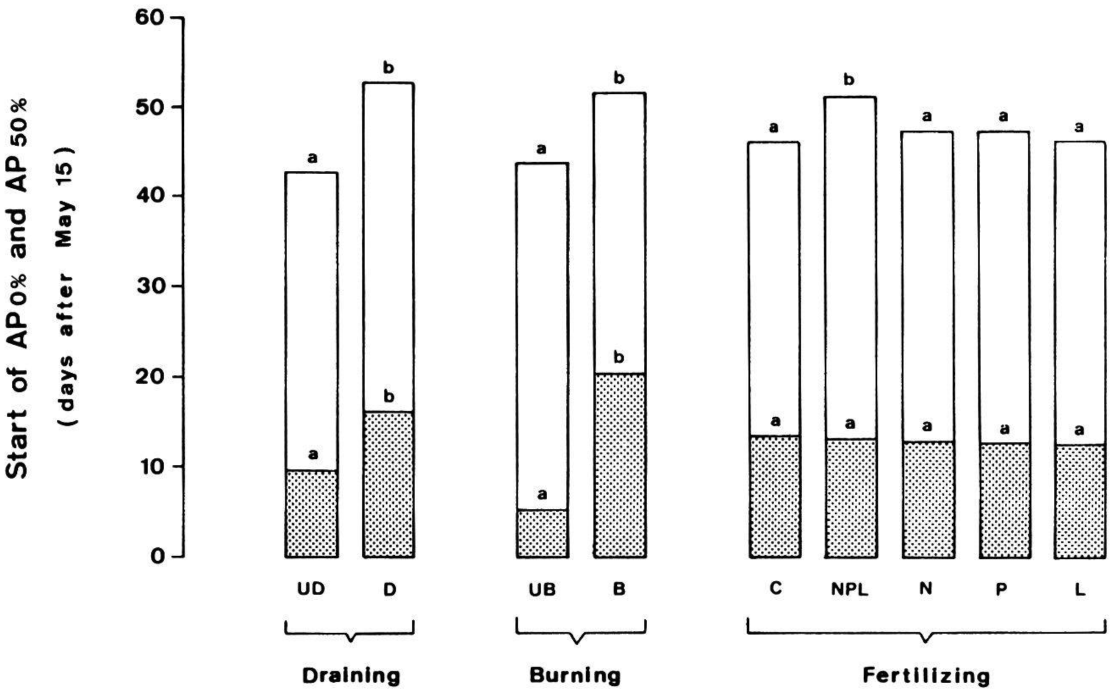


Fig. 23. Start of the assimilation periods 50% (AP 50%, shaded portion) and 0% (AP 0%, entire bars) of Typha glauca under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** 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 reduc-

tions 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

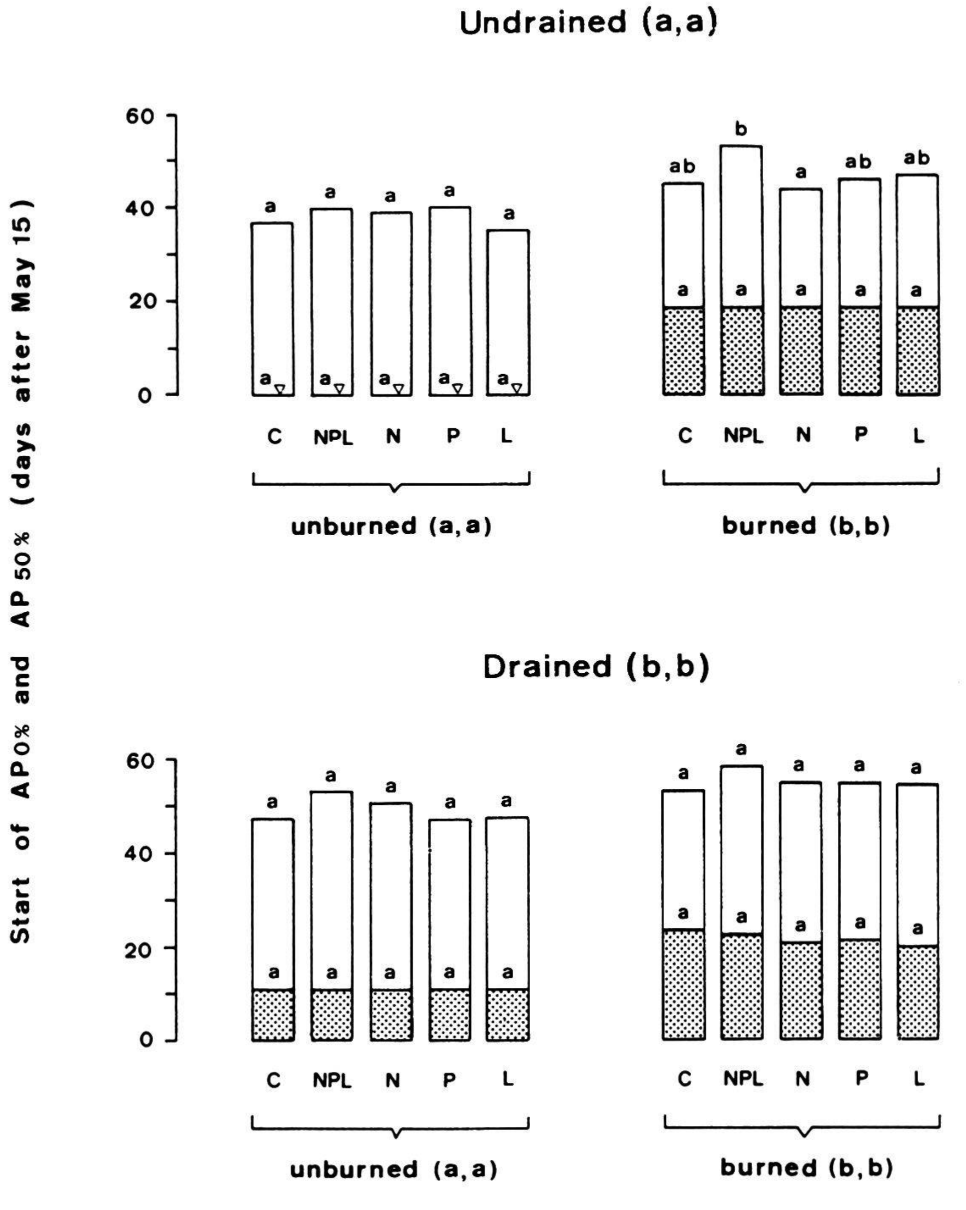


Fig. 24. Start of the assimilation periods 50% (AP 50%, shaded portion) and 0% (AP 0%, entire bars) of Typha glauca in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Values are means n = 5. Two draining treatment means (all burning and ferilizer 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 <u>Typha</u> 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 <u>Typha</u> plants in the NPL-plots reached 50% of their final height later than the <u>Typha</u> 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 <u>Typha</u> 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-

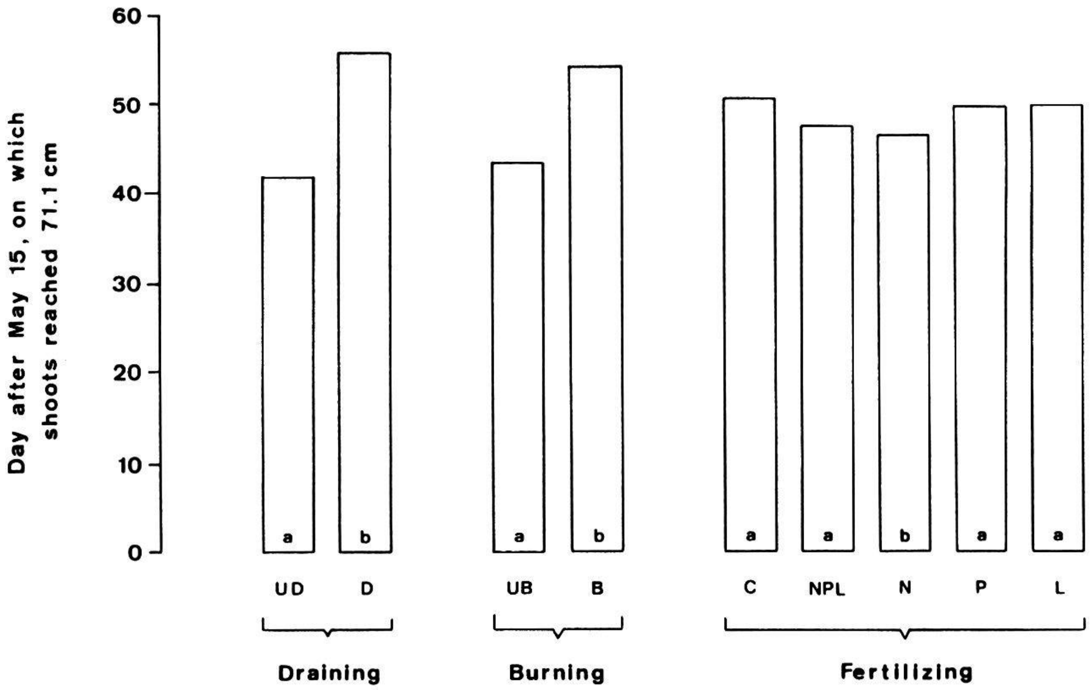


Fig. 25. Day after May 15, on which mean shoot height of Typha glauca reached 71.1 cm, that is 50% of the final height in the undrained, unburned and unfertilized treatment plots, under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all 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

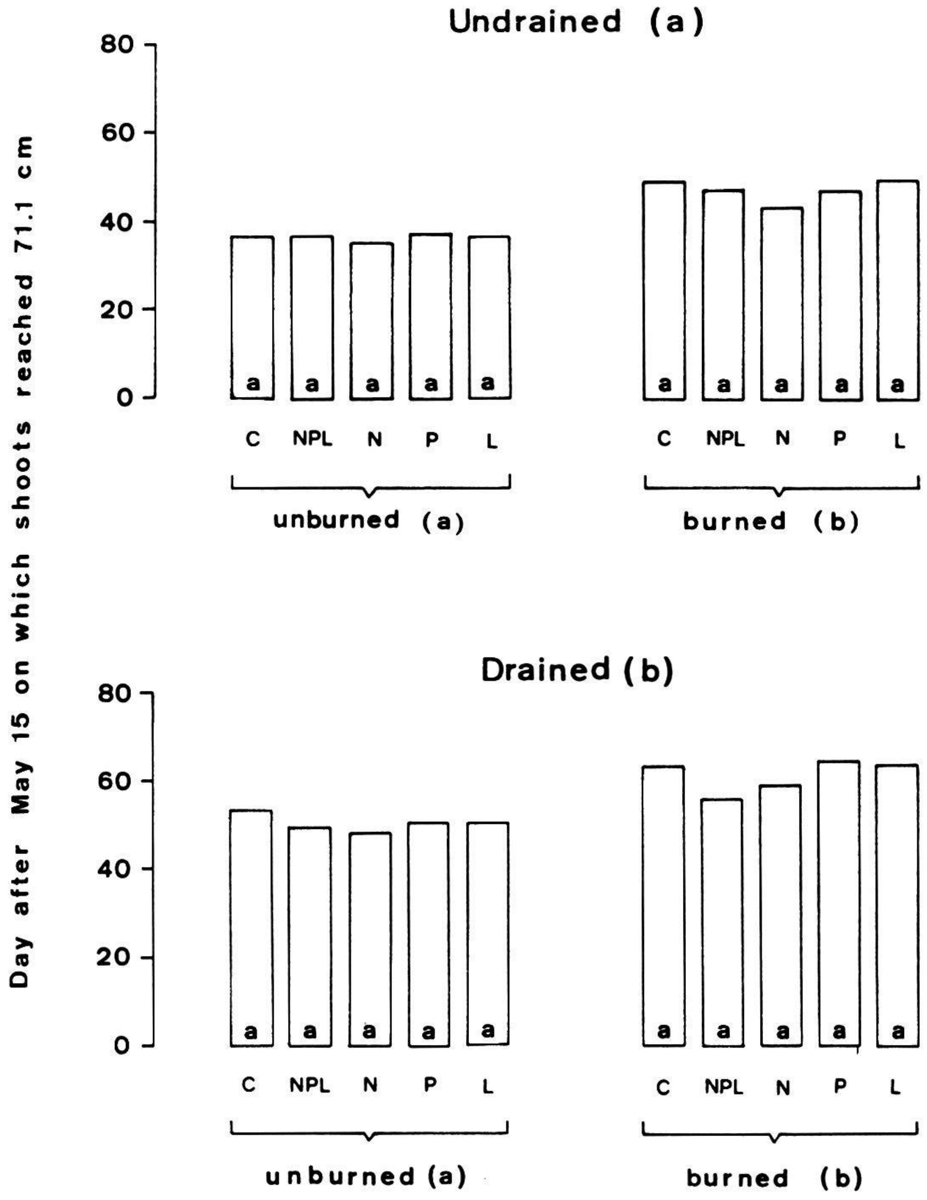


Fig. 26. Day after May 15, on which mean shoot height of Typha glauca reached 71.1 cm, that is 50% of the final height in the undrained, unburned and unfertilized treatment plots, in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: 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

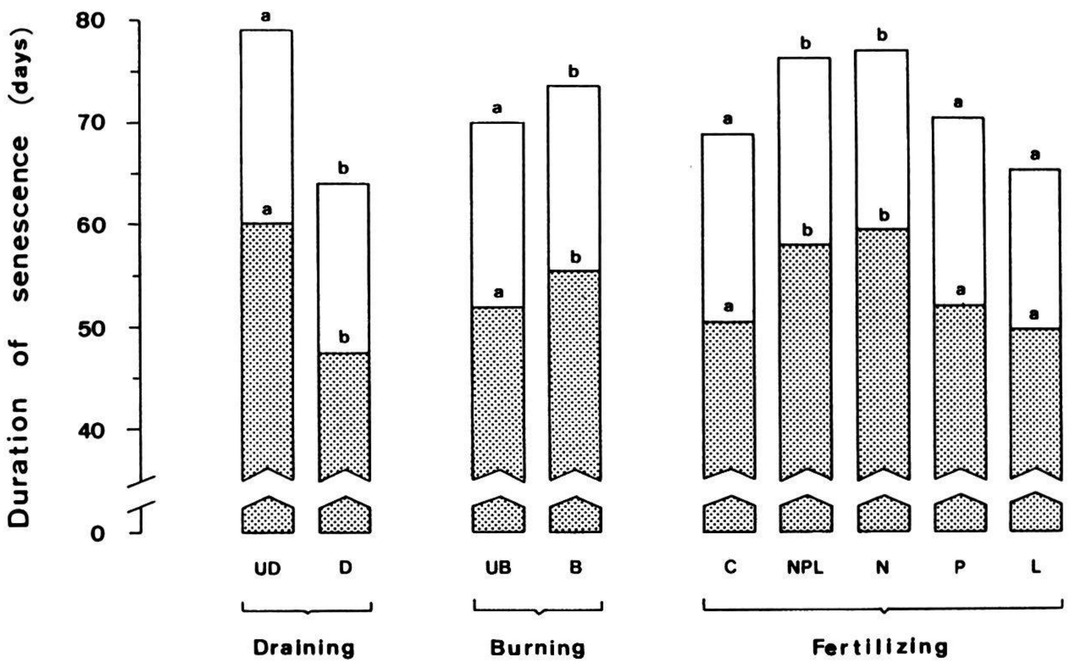


Fig. 27. Duration of senescence 50% (DS 50%, shaded portion) and 100% (DS 100%, entire bars) of Typha glauca under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: 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,

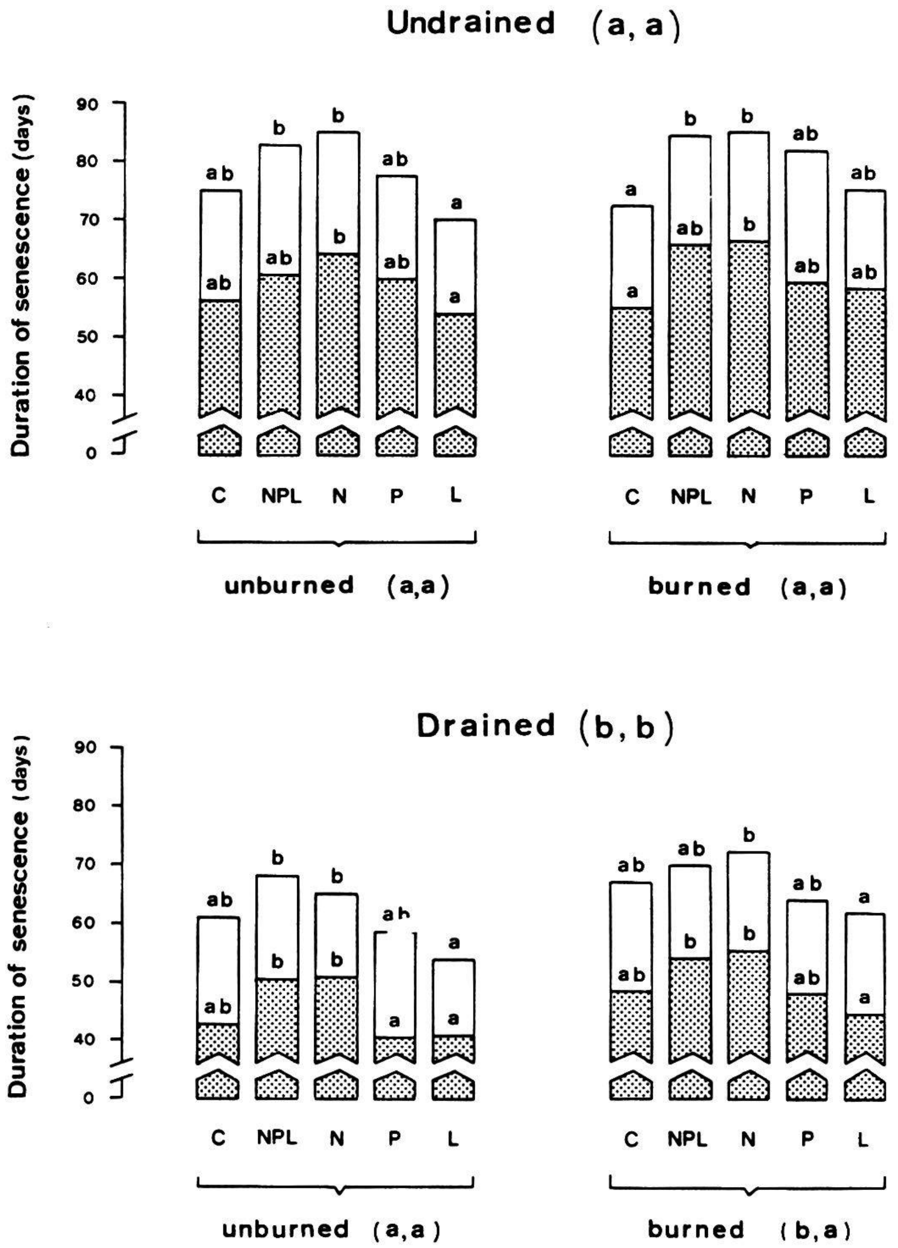


Fig. 28. Duration of senescence 50% (DS 50%, shaded portion) and 100% (DS 100%, entire bars) of <u>Typha glauca</u>, in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Values are means n = 5. Two draining treatment means (all burning and fertilizer 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.

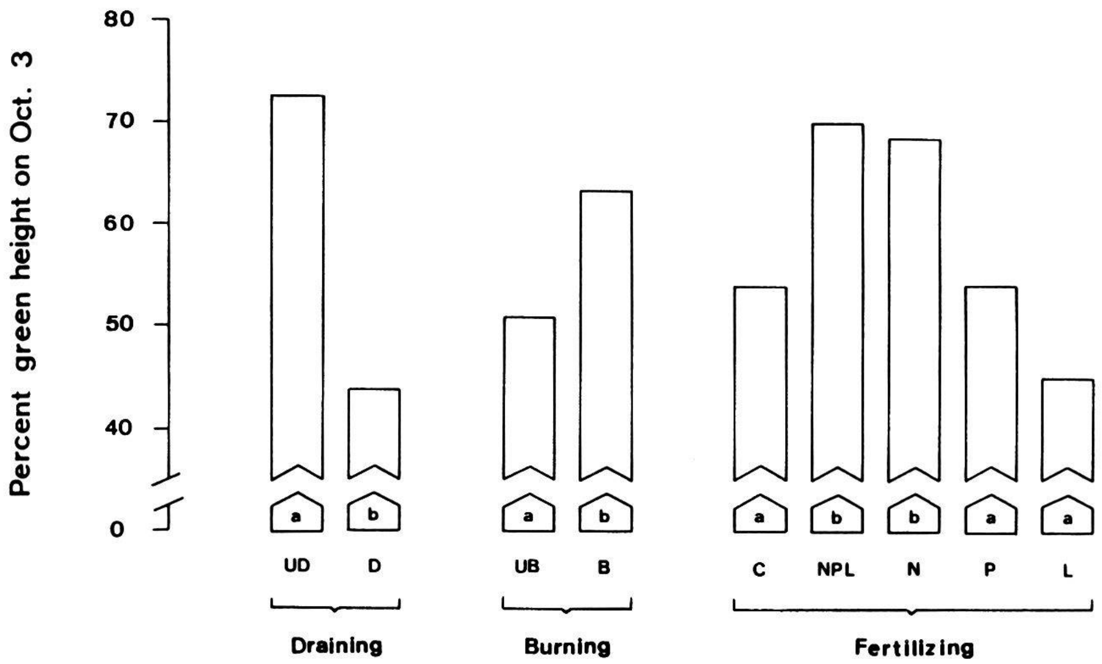


Fig. 29. Height of the green shoot portion of Typha glauca on October 3, in percent of total shoot height, under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; 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

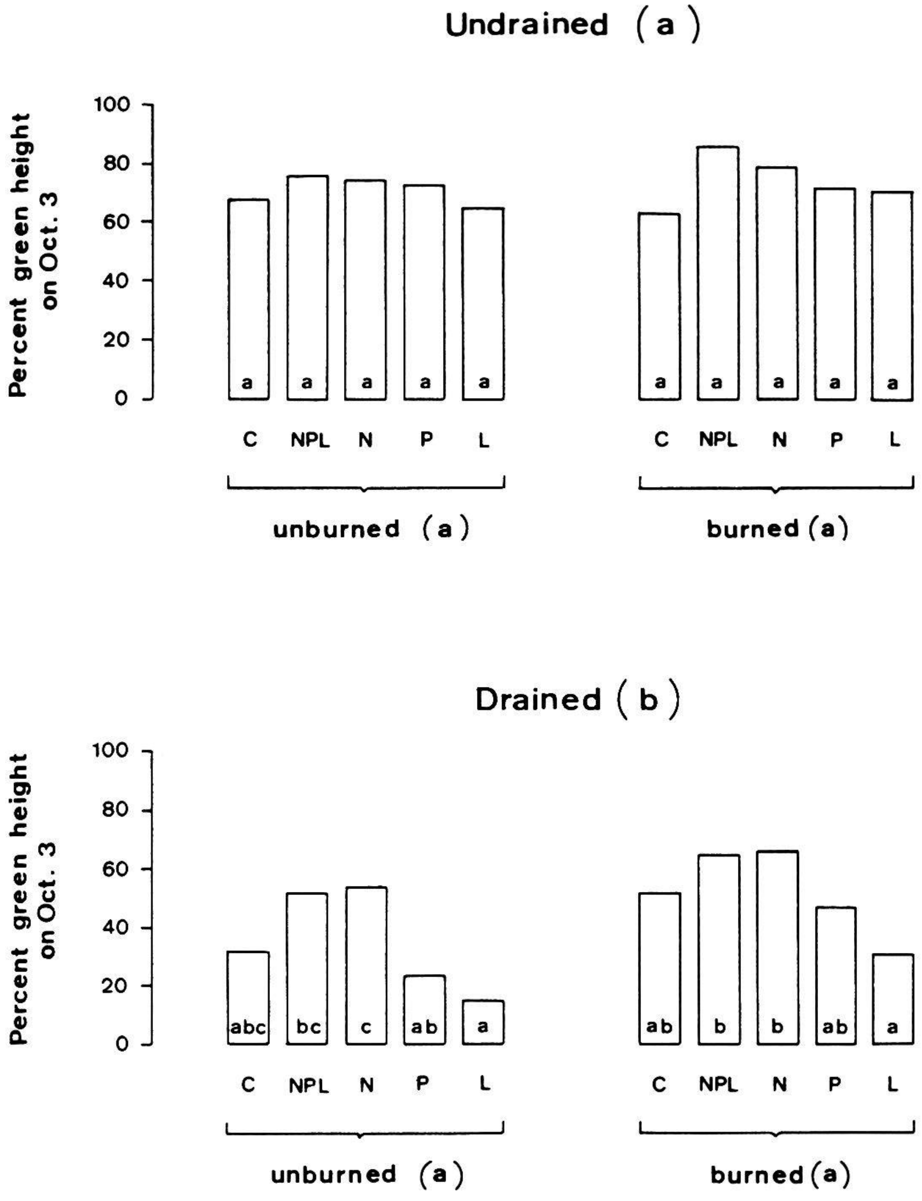


Fig. 30. Height of the green shoot portion of <u>Typha glauca</u> on October 3, in percent of total shoot height, in response to different fertilizer treatments which were superimposed on four draining x burning regimes.

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

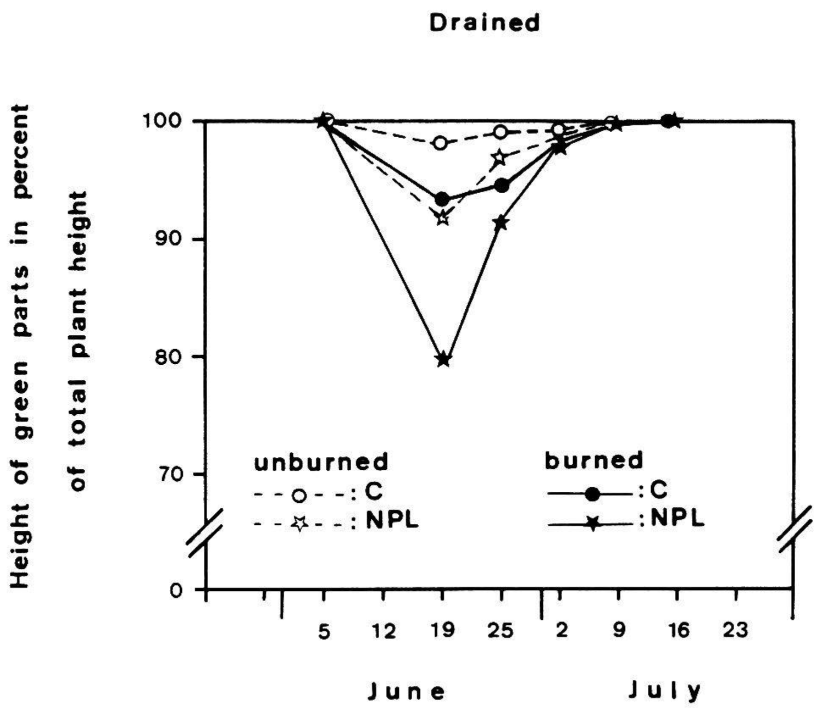


Fig. 31. Susceptibility of Typha glauca to drought: Height of green parts in percent of total plant height, during June and July 1982, in the drained treatment on which were superimposed burning and fertilizer treatments.
C: unfertilized; NPL: nitrogen, phorphorus and lime added. Values are means n =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

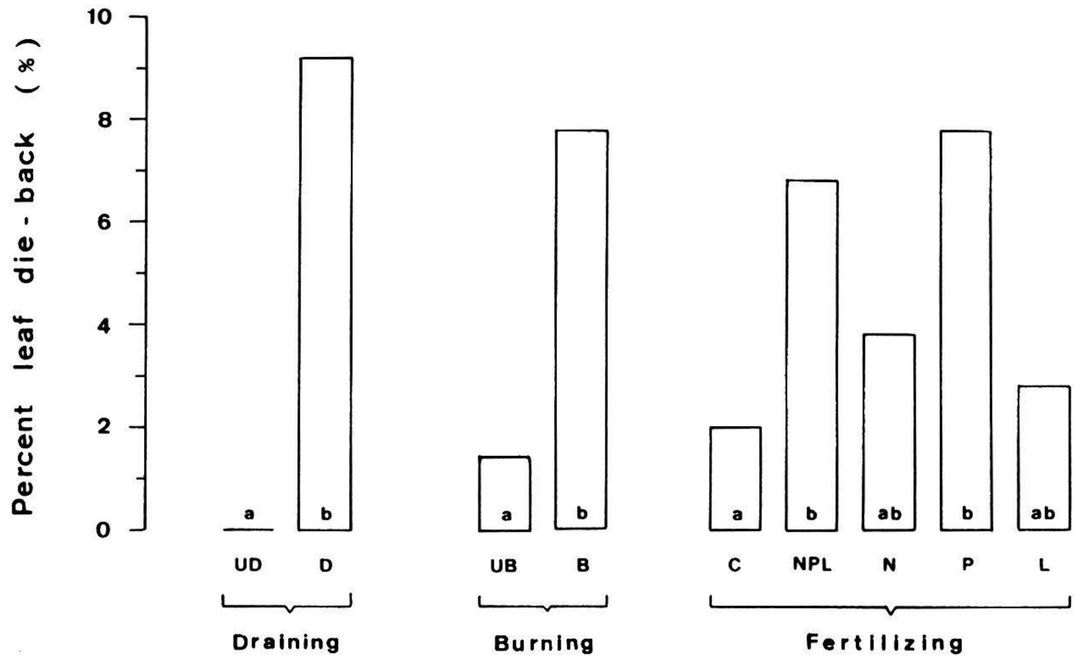


Fig. 32. Susceptibility of Typha glauca to drought: Leaf die-back on June 19 in percent of total plant height, under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: 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).

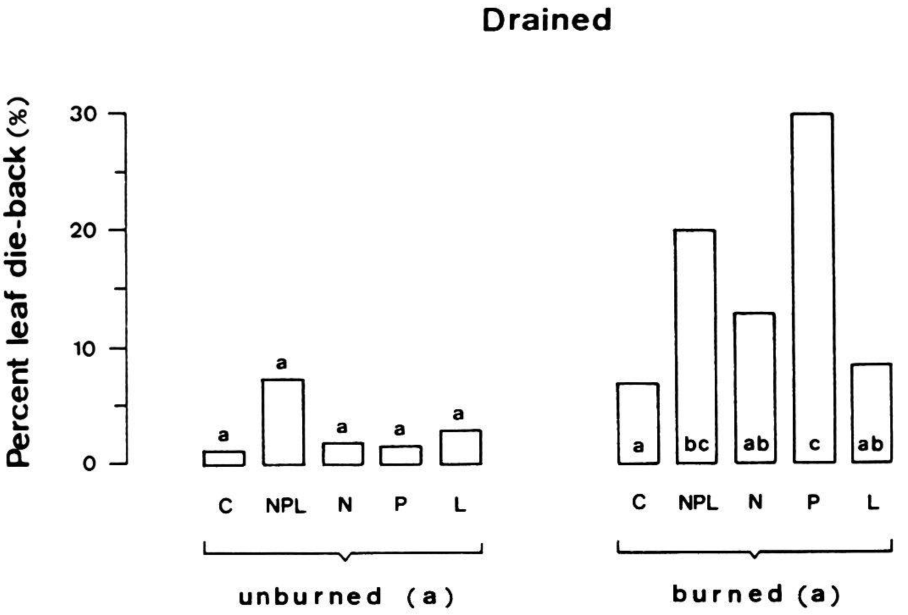


Fig. 33. Susceptibility of Typha glauca to drought in the drained basin: Leaf die-back on June 19 in percent of total plant height, in response to different fertilizer treatments which were superimposed on two burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime 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 above-ground 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).

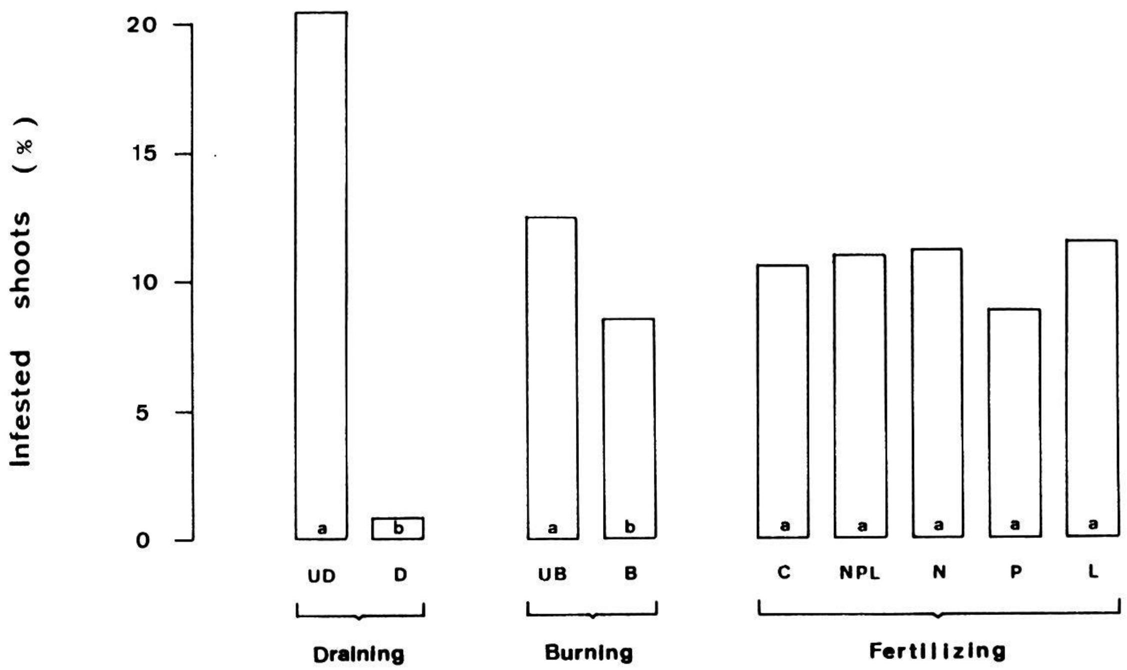
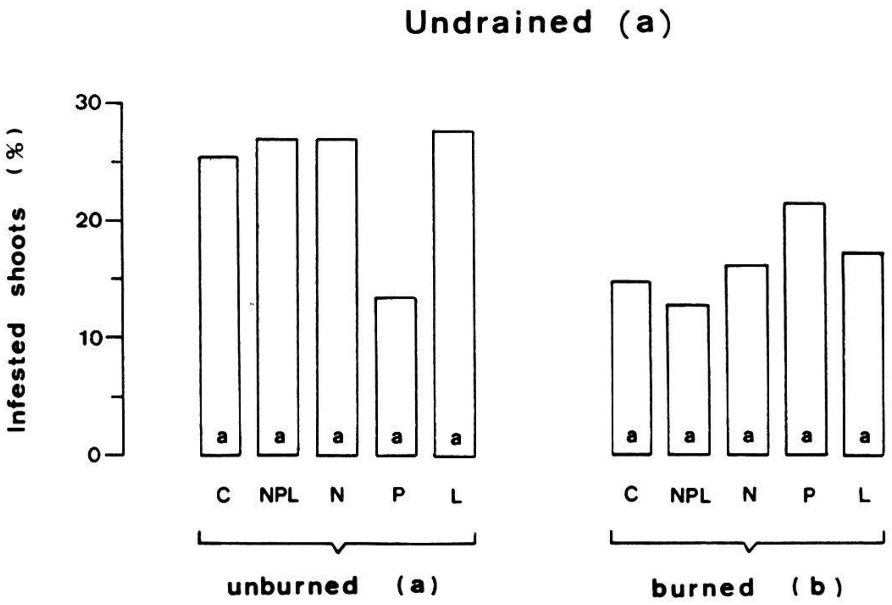


Fig. 34. Insect damage: Percentage of Typha glauca shoots attacked by stem-boring insect larvae, under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: 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).



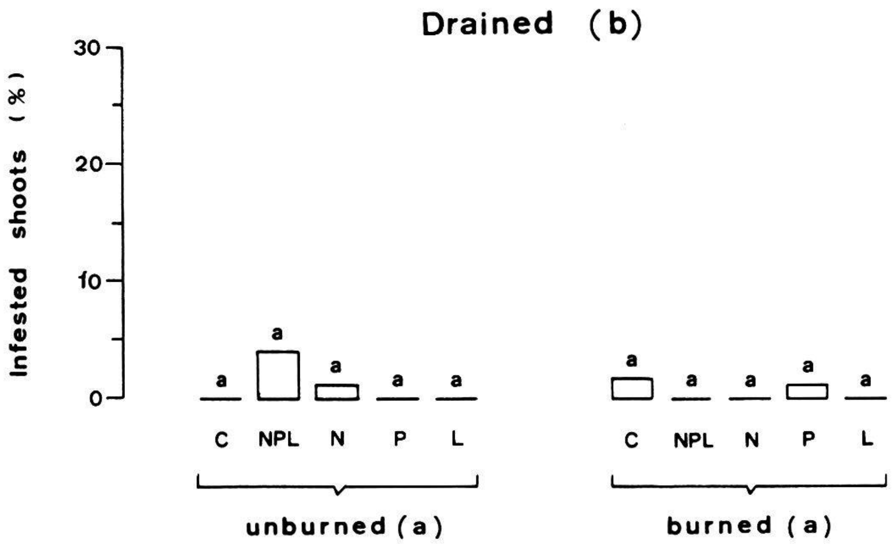


Fig. 35. Insect damage: Percentage of Typha glauca shoots attacked by stem-boring insect larvae, in response to different fertilizer treatments which were superimposed on four draining x burning regimes.

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

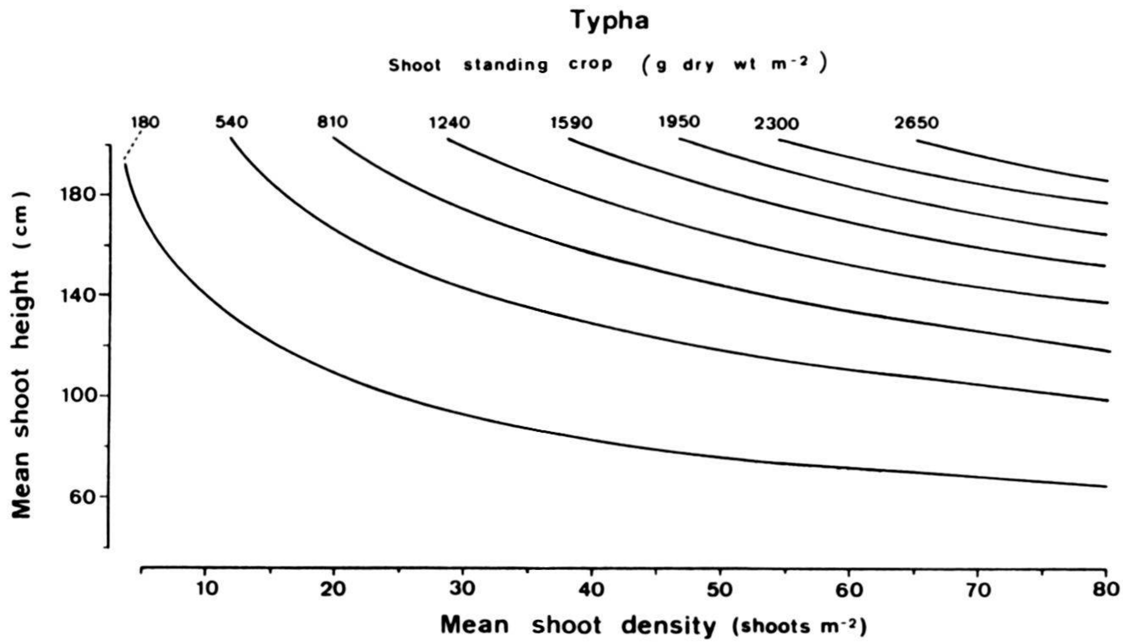


Fig. 36. Shoot standing crop (S) of Typha glauca (g dry weight/m^2) as predicted from mean shoot height (H) and mean shoot density (D) (contour plot). The regression equation $\ln(S) = -9.26288 + 2.4953*\ln(H) + 0.93681*\ln(D)$ explained 94.2% of the variance ($P<0.001$).

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).

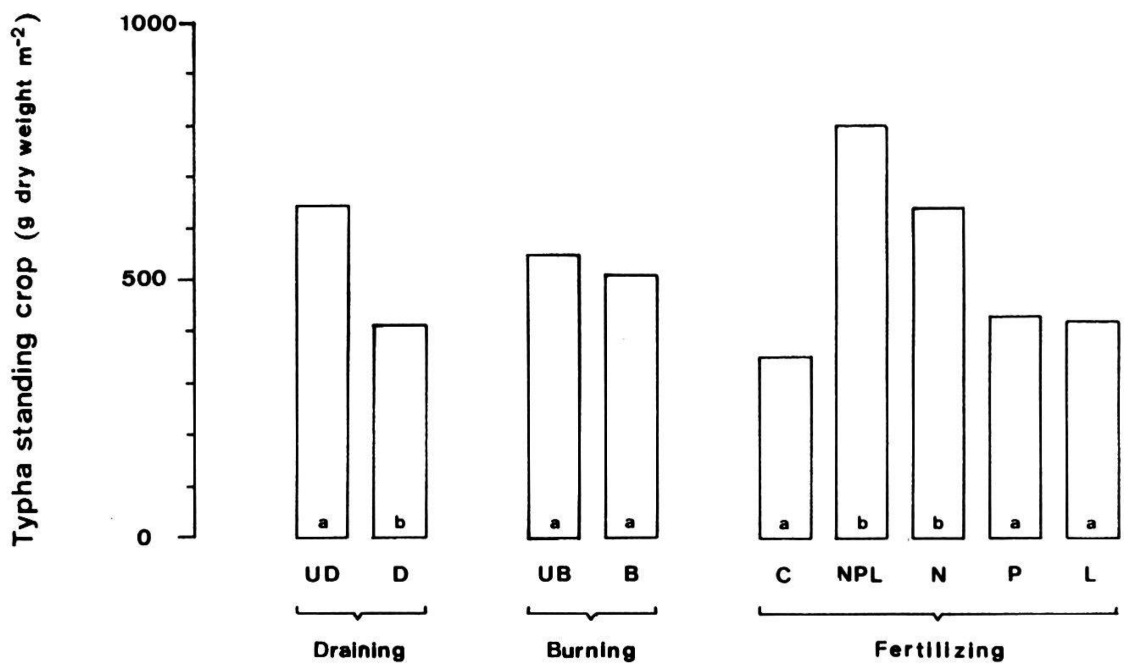


Fig. 37. Shoot standing crop of *Typha glauca* (g dry weight/m^2) under different draining, burning and fertilizer treatments.
Draining treatments: UD: undrained; D: drained; n = 50; all burning and fertilizer treatments combined. **Burning treatments:** UB: unburned; B: burned; n = 50; all draining 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).

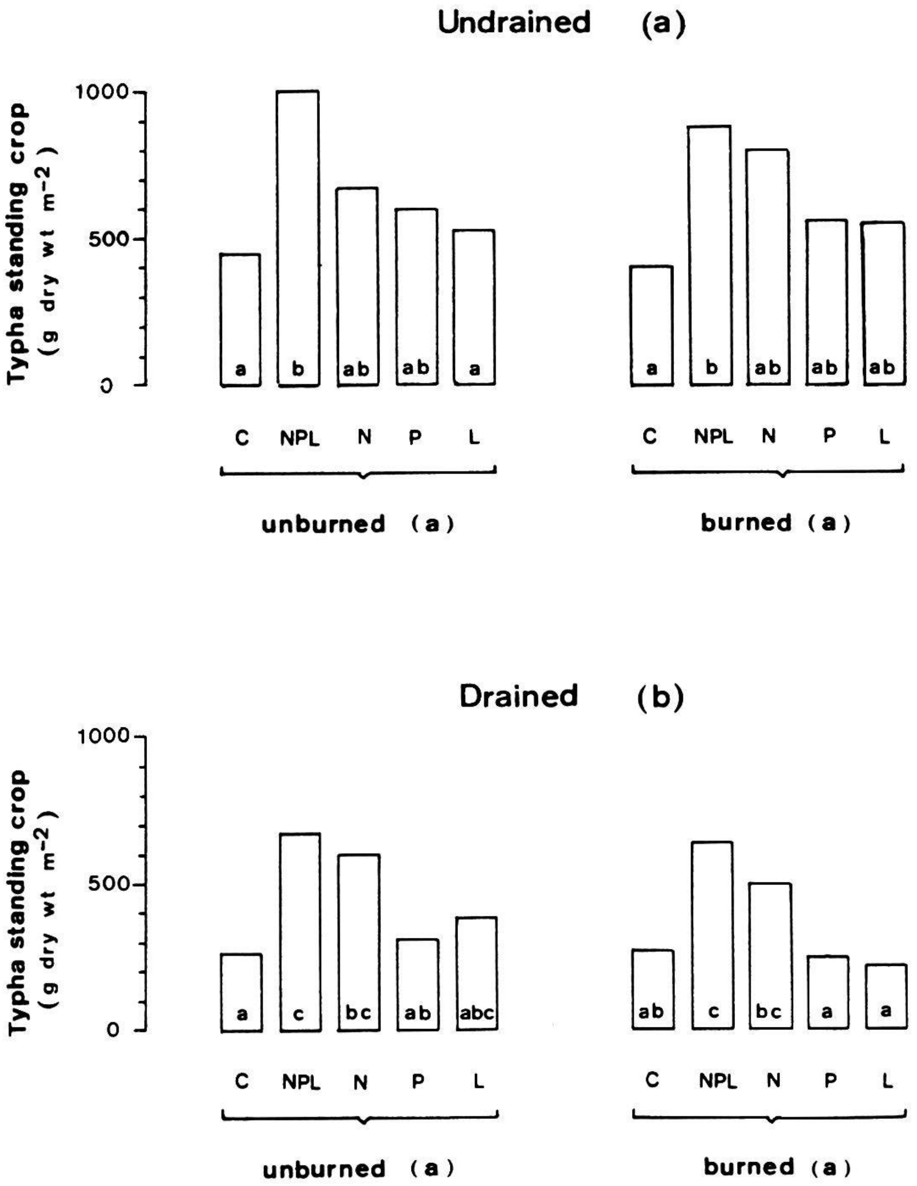


Fig. 38. Shoot standing crop of Typha glauca (g dry weight/m^2) in response to different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; N: nitrogen added; P: phosphorus added; L: lime 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.

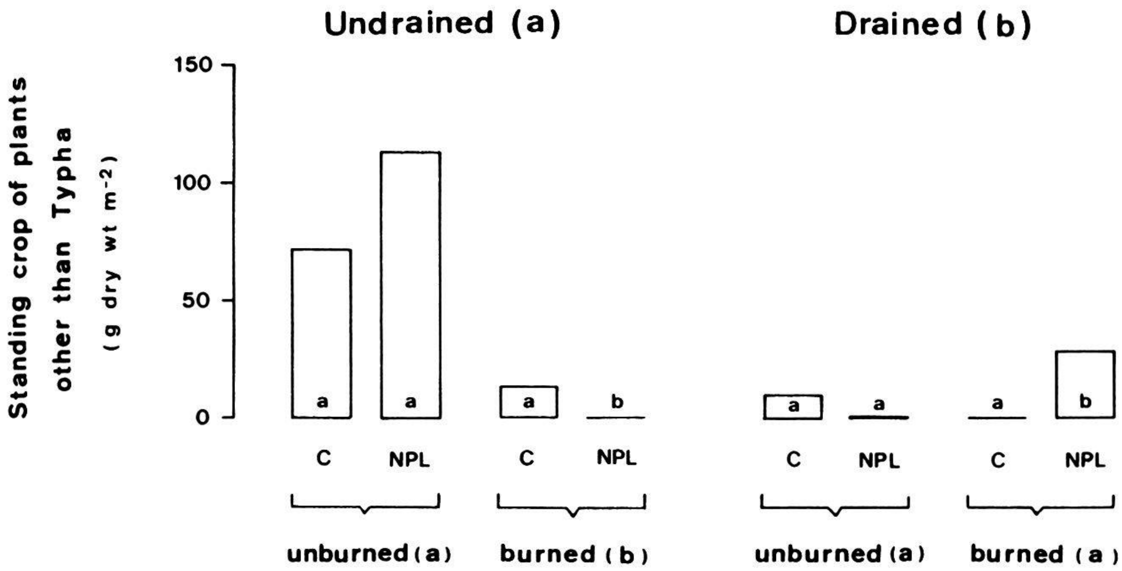


Fig. 39. Aboveground standing crop of plants other than Typha (g dry weight/m^2) under two different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; n = 5) Two draining means (all burning 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

Typha 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;

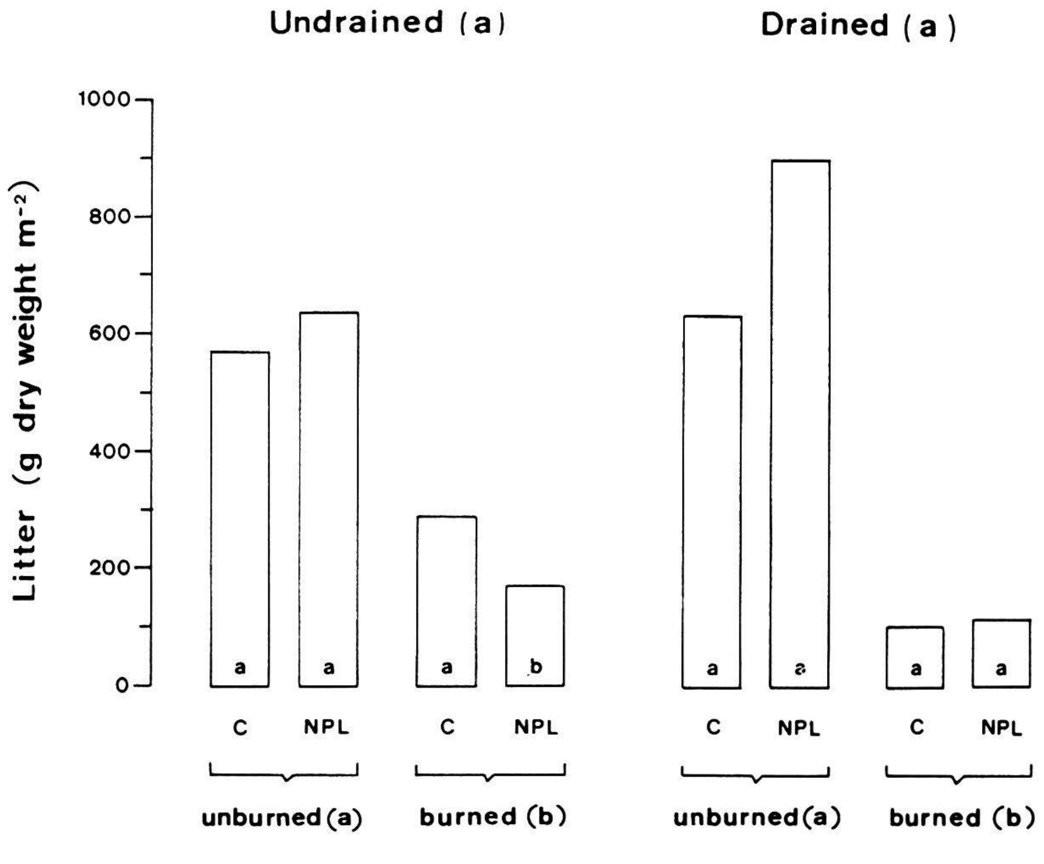


Fig. 40. Litter load (g dry weight/m^2) under two different fertilizer treatments which were superimposed on four draining x burning regimes.
Fertilizer treatments: C: unfertilized; NPL: nitrogen, phosphorus and lime added; n = 5) Two draining means (all burning and fertilizer treatments combined; n = 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).