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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 domin-
gensis 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°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°C, respectively, than at 18°C. SHARITZ et al. (1984) reported for Typha latifolia and Typha do-
mingensis 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., $n = 10$) $^{\circ}\text{C}$ vs. 13.8 ± 0.1 $^{\circ}\text{C}$ for the period of June 12 to July 12 and 21.0 ± 1.4 $^{\circ}\text{C}$ vs. 23.6 ± 0.9 $^{\circ}\text{C}$ 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 above-mentioned 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 Typha glauca 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 Typha 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., Typha growth was expected to increase less dramatically in undrained-burned than in drained-burned treatments. However, no such increase in Typha productivity was observed in the present study, neither in the drained nor in the undrained basin. Burning did not significantly alter current years Typha 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 Typha glauca 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 (SKUHRVY 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 signifi-

cantly 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 Phragmites, 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 to 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 and 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., $n = 21$) °C vs. 24.6 ± 1.3 °C and 21.4 ± 0.9 °C vs. 12.8 ± 0.8 °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., $n = 10$) $^{\circ}\text{C}$ vs. 11.2 ± 0.3 $^{\circ}\text{C}$ for the drained and 14.1 ± 0.3 $^{\circ}\text{C}$ vs. 13.8 ± 0.1 $^{\circ}\text{C}$ 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 study 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/m² with an average of 1156 g/m². And shoot standing crops reported by other authors were, in increasing order, 946 g/m² in central Minnesota (BERNARD and BERNARD 1973), 1320 g/m² in New Jersey (WHIGHAM and SIMPSON 1976), 1360 g/m² in Minnesota (BRAY 1962), 1361 g/m² in central New York (BERNARD and FITZ 1979), 1565 g/m² in New Jersey (JARVIS 1969) and 1680 g/m² 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/m² for Typha latifolia in South Dakota (McNAUGHTON 1966) up to 4040 g/m² 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

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/m² in NPL-fertilized vs. 0 g in unfertilized plots

Parameter	Difference MPL-fertilized vs. unfertilized					
	All draining and burning treat- ments 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 DYKYOVA (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 phosphorus-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	+ 23.9%	NS
4) Shoot density on June 19 in percent of final shoot density	- 9.3%	NS	- 19.3%	*	+ 17.9%	NS
5) Final shoot density	+ 13.0%	NS	- 15.2%	NS	- 3.2%	NS
6) Shoot height on June 19	+ 6.6%	NS	- 1.8%	NS	+ 8.9%	NS
7) Final shoot height	+ 17.1%	***	+ 13.7%	NS	+ 22.8%	*
8) Basal shoot circumference	+ 35.0%	***	+ 33.8%	**	+ 50.3%	***
9) Number of leaves per shoot	+ 16.5%	***	+ 15.2%	*	+ 30.5%	***
10) Length of the assimilation period 0%	+ 5.9%	***	+ 6.2%	*	+ 2.8%	NS
11) Length of the assimilation period 50%	+ 7.8%	***	+ 5.2%	NS	+ 6.3%	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	+ 2.7 days	NS
14) Day after May 15 on which shoot height reached 71.1 cm	- 4.1 days	**	- 1.6 days	NS	- 5.1 days	NS
15) Duration of senescence 50% (yellowing halfway through)	+ 8.6 days	***	+ 8.0 days	*	+ 8.1 days	*
16) Duration of senescence 100% (yellowing complete)	+ 7.9 days	***	+ 10.2 days	*	+ 3.9 days	NS
17) Green height in percent of total height on October 3	+ 26.9%	**	+ 10.2%	NS	+ 68.1%	*
18) Susceptibility to drought (percent leaf die-back on June 19)	+ 90.1%	NS	0.0%	NS	+ 63.6%	NS
19) Insect damage(percent infested shoots)	+ 6.0%	NS	+ 6.5%	NS	+ 8.0%	NS
20) Typha shoot standing crop on June 19	- 13.3%	NS	- 31.6%	NS	+ 60.0%	NS
21) Typha shoot standing crop in Oct./Nov.	+ 85.7%	***	+ 50.7%	NS	+ 129.7%	*
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

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
	← Start of emergence before phosphorus was added → ← Application of phosphorus on June 13 →					
1) Start of shoot emergence						
2) Shoot density on June 12						
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%						
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.						
23) Litter load in Oct./Nov.						
	← no measurements → ← 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 KERÉKES (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

Table 9 (page 98). The effect of fertilizing with **phosphorus** (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 = $P > 0.06$

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%	+ 16.4%	NS	+ 53.0%
4) Shoot density on June 19 in percent of final shoot density	+ 10.1%	NS	- 11.8%	NS	+ 1.7%	NS
5) Final shoot density	+ 13.4%	NS	+ 3.4%	+ 35.9%	NS	+ 34.7%
6) Shoot height on June 19	+ 5.4%	NS	- 2.9%	NS	+ 7.0%	NS
7) Final shoot height	+ 2.3%	NS	- 3.0%	NS	+ 3.1%	NS
8) Basal shoot circumference	- 4.0%	NS	- 4.7%	NS	- 9.9%	NS
9) Number of leaves per shoot	- 1.8%	NS	- 0.8%	NS	- 3.3%	NS
10) Length of the assimilation period 0%	- 1.8%	NS	- 2.8%	NS	- 5.1%	NS
11) Length of the assimilation period 50%	- 1.3%	NS	- 0.3%	NS	- 2.0%	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	+ 1.6 days	NS	+ 0.6 days
14) Day after May 15 on which shoot height reached 71.1 cm	- 0.4 days	NS	- 0.4 days	+ 0.7 days	NS	+ 0.7 days
15) Duration of senescence 50% (yellowing halfway through)	- 1.1 days	NS	- 2.1 days	+ 3.3 days	NS	- 3.9 days
16) Duration of senescence 100% (yellowing complete)	- 3.6 days (*)		- 4.6 days	+ 3.0 days	NS	- 5.6 days
17) Green height in percent of total height on October 3	- 16.1%	NS	- 4.7%	+ 11.6%	NS	- 40.8%
18) Susceptibility to drought (percent leaf die-back on June 19)	+ 40.0%	NS	0.0%	NS	+ 154.5%	NS
19) Insect damage (percent infested shoots)	+ 10.1%	NS	+ 9.1%	+ 16.5%	NS	- 100.0%
20) Typha shoot standing crop on June 19	+ 3.2%	NS	- 18.9%	+ 24.9%	NS	+ 55.2%
21) Typha shoot standing crop in Oct./Nov.	+ 22.0%	NS	+ 20.0%	+ 38.0%	NS	- 21.3%
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 MELILLO (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

Table 10 (page 100). The effect of **liming** at a rate of 625 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 = $P > 0.06$

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 standing 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.