directie flevoland



nitrogen and phosphorus economy of reed vegetation in the polder zuidelijk flevoland (the netherlands)

m.j.h.a. van der linden



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rapporten inzake de inrichting en ontwikkeling van de ijsselmeerpolders en andere landaanwinningswerken

flevoberichten zijn bedoeld als communicatiemiddel t.b.v. degenen die betrokken zijn bij het werkterrein van de directie flevoland; de conclusies kunnen van voorlopige aard zijn, omdat het onderzoek nog niet kan zijn afgesloten.

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Preface

After drainage of an IJsselmeerpolder the rapid succession of the pioneer vegetation resulting in a closed reed stand is accelerated by sowing reed. Reed grows luxuriantly on the fertile, initially waterlogged soil, covering within two to three years all the area with a tall, dense growth, suppressing most other kinds of wild plants. As early as in the fifties research on reed already started in the Noordoostpolder, in particular with respect to such practical aspects as eradication of the reed during reclamation, appearing to be rather easy after the installation of a subsurface drainage system. Knowledge on the natural development of the reed vegetation under various environments was essential both for management and eradication of the reed. Trials were laid out with various depths of the groundwater table, as reed does not thrive well at too dry conditions, and various ways of management. Experience also showed, that the reed degenerated in the course of time, among other things due to damage by stemboring insects. But also a shortage in nutrients might have been involved. Considering the vast areas under natural conservancy, covered by reed and partly by other herbaceous plants and to be managed in any way, insight in the nutrient cycle of the present natural vegetation was important. For this reason, the author of the present paper, working with the Research Institute for Nature Management (RIN) at Leersum (The Netherlands) and experienced in this type of work, was charged with this research. The results are presented in this paper.

> Ir. C.D. van der Wildt Managing Director Directorate Flevoland Rijkswaterstaat

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Abstract

Nitrogen and phosphorus economy of reed vegetation in the polder Zuidelijk Flevoland / M.J.H.A. van der Linden; Research Institute for Nature Management - Rijksinstituut voor Natuurbeheer (RIN). - Lelystad: RWS, Fl, 1990. - 50 pp.: fig., tab.; 30 cm. = (Flevobericht; 313) Ref.: ISBN 90-369-1066-8

N and P shortages might have explained the expected degeneration of closed stands of reed developed a few years after emergence of the polder in 1968. Distribution of N and P among shoots and *rhizomes* was determined to estimate the extent of internal recirculation of N and P. The nitrate-reductase activity of the shoots and the numbers of NH₄-oxidizers at various water levels gave indications about the availability of nitrate. N losses by denitrification over the 1968-1975 period were assessed from tentative N budgets based on the uptake of N by the reed vegetation - including N losses due to burning in early spring - and the decrease of total soil N in the top 1 m of the soil as well as of mineral N down to the pleistocene sand at about 3 m depth. The points of time, up till when no N and P shortages are expected, were based on the stock of mineral N and citric acid-soluble P in the top 2 m of the soil in 1975, respectively, and the uptake of N and P by the vegetation since 1968.

Summary

Nitrogen and phosphorus economy was investigated as part of a study on the reed (*Phragmites australis* (Cav.) Trin. ex Steudel) vegetation in the newly reclaimed polder Zuidelijk Flevoland. The present investigation concentrated on highly productive stands of reed on clay soil, that were burned annually. Decrease of shoot N and P in the second half of the growing season in 1974 and 1975 was coupled with an increase of rhizome N and P. Development of the new shoots in the first half of the growing season was coupled with a decrease of rhizome N and P. Loss by seed and losses due to leaching by rain could explain at most 20% of the N and P decrease in the shoots from August onward. Under the assumption that the remaining seasonal changes of shoot and rhizome N and P were due to internal recirculation, it was concluded that between 25 and 50% of the about 200 kg N and about 40% of the 20 kg. ha⁻¹.y⁻¹ P required for shoot growth originated from the previous year's shoots after storage in the rhizomes. The yearly N loss due to burning of the old shoot mass in early spring was estimated to be considerable with 90 kg. ha⁻¹ N, i.e. 65% of the N left in the previous year's shoots.

Numbers of NH⁴₄-oxidizers in the soil tended to be higher when the water table was low. This trend was coupled with higher levels of nitrate and nitrate-reductase activity in the shoots, indicating that part of the N was taken up as NO₃-N. the concentration of NH⁴₄-oxidizers down to a depth of 2 m corresponded in order of magnitude with that in the top layer of fertile calcareous soils. Considerable numbers of NH⁴₄-oxidizers were found to be still present in the permanently water-saturated subsoil several years after removal of the reed vegetation. This suggests that they had survived in an inactive state, because in the absence of reed shoots there was no oxygen supply. From the nitrate-reductase activity in the shoots at various water levels in the soil it was concluded that nitrification was of limited significance, especially in the anaerobic sub-soil, notwithstanding the presence therein of not negligible numbers of nitrifiers, living roots of reeds and large amounts of ammonium.

The 1200 kg. ha⁻¹ N that was incorporated into rhizomes, larger roots, and the above-ground reed during the 1968-1975 period originated mainly from the stock of mineral N already present in 1968, when the area emerged and the reed was sown. In 1975, the upper 2 m of the soil still contained enough 1N K₂SO₄ extractable mineral N to meet the requirements for at least three seasons of fire-managed reed growth. Fixed NH₄⁺-N, and also soil N mineralized from 1968 onward hardly contributed to the above-mentioned 1200 kg. ha⁻¹ N. Retrieval of N from the partially burned litter was insignificant, amounting to 20 kg. ha⁻¹ N in 1975. From tentative N budgets over the 1968-1975 period a denitrification loss of as little as 100 kg. ha⁻¹ N was calculated. the loss occurred during the first four years after emergence. It was concluded that the production of nitrate had not considerable exceeded the uptake capacity of the reed.

On the basis of data referring to the 1968-1975 period, the mean P requirement of the reed was estimated to be 25 kg. $ha^{-1}.y^{-1}$ soil P. In view of the stock of citric acid-soluble phosphate down to a depth of 2 m, P shortage would not be expected within four decades starting in 1968.

1. Introduction

Management of natural vegetation is often focussed on nutrient availability. Studies on the pathways along which wild plants in an undisturbed environment are supplied with nutrient can provide useful background information for this management. The recently reclaimed polder Zuidelijk Flevoland offered an opportunity to study the N and P economy of the reed vegetation. The investigation reported in this paper was part of a study on the factors governing the development of this vegetation (van der Toorn & Mook, 1982; Mook & van der Toorn, 1982, 1985).

In the new IJsselmeerpolders a closed stand of common reed can have developed within a few years after drainage. To promote the establishment of a dense reed vegetation in order to make the new land suitable for agricultural purposes sooner, reed is sown. In the older polder Oostelijk Flevoland a marked decrease in production occurred four to five years after closed stands had developed. In addition to water shortage and damage by insects, which can be eliminated by burning, the depletion of N and (or) P could possibly explain the reed degeneration, which was expected to occur in the polder Zuidelijk Flevoland as well.

There are many reports on late-season translocation of nutrients from dying foliage to perennial plant parts, especially in respect to trees and shrubs (Chapin, 1980; Staaf, 1982; Chapin & Kedrowski, 1983). N retrieval from senescent foliage ranges between nil and 75%, whereas for P this range lies between nil and 89%. At present there is no clear evidence that species adapted to infertile soils are particularly effective in retracting nutrients prior to leaf abscission (Chapin, 1980; Staaf, 1982). Obviously information about internal translocation can improve estimation of the effect of management practices, such as mowing, intended to remove nutrients from natural vegetations.

Six to nine years after emergence, rather high N dressings were required in the Noordoostpolder to obtain maximum wheat production (Van Schreven, 1957). The limited availability of N in the Usselmeer polders which originally had large amounts of mineral N in the soil was ascribed to losses related to the establishment of the pioneer vegetation in the first years after emergence and to low decomposition rates of the original soil organic matter (Van Schreven, 1963^a, 1963^b, 1963^c). In reed stands of the polder Oostelijk Flevoland more mineral N had disappeared from the soil during the first three years after emergence than was taken up by the vegetation (Van Schreven, 1963°). The observed N losses were ascribed to denitrification following mineralization of fresh reed material in the semiaerobic upper soil layers. Several species of bog plants release oxygen from roots (Armstrong, 1964; Black, 1968). In the unripened water-saturated black soil layers of the Flevoland reed fields, brown spots were often seen in the vicinity of roots. The brown discoloration is due to iron hydroxides resulting from oxidation of iron sulphides (De Glopper, 1973) and indicates oxygen release from the reed roots. Local availability of oxygen in the anaerobic subsoil with a high NH4-N content (Van Schreven, 1963^a) could result in a nitrification-denitrification sequence, as found in wet rice fields after ammonium fertilization (Garcia, 1975^a, 1975^b). Thus, apart from N losses due to burning, losses by denitrification could seriously influence the performance of reed in the IJsselmeerpolders.

The purpose of the present study was to explain the N and P supply of the reed vegetation on the basis of internal retrieval, retrieval from the litter layer and losses and availability in the mineral soil. Results on internal N and P retrieval, N losses due to fire management, and availability of P in the soil have already been published elsewhere (Van der Linden, 1980, 1986).

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2. Materials and methods

2.1. Study area

The study area was located in parcel Nz 17 of the Zuidelijk Flevoland polder (fig. 2.1.). The reed (*Phragmites australis* (Cav.) Trn. ex Steudel) was sown by aeroplane in 1968, when Zuidelijk Flevoland gradually became dry. The soil was a calcareous heavy clay, containing 5-10% and 10-20% humus in the 0-75 and 75-200 cm layer, respectively (Van der Toorn, unpubl.). In 1971, when the area had an almost closed reed vegetation, various experimental plots were set up in parcel Nz 17. Wet areas were created by irrigation, embankments allowing a water level of at most 20 cm above the surface in these areas (Table 2.1.). Generally, the groundwater level in the dry areas varied between 40 and 100 cm below the surface in the summer and between 30 and 80 cm in the winter. In the course of the 1968-1975 period the fluctuations within these ranges became larger after the ripened depth of the soil profile had increased and more rainwater could be stored in the soil. Burning



Figure 2.1. Schematic representation of the experimental reed field and map showing the location of parcel Nz 17 in the polder Zuidelijk Flevoland

Table 2.1 Variation of water level in the experimental plots; the winter levels refer to the period from about 1 November until burning in March or April and the summer levels to the rest of the year. Levels are given in cm below (-) or above (+) the surface

	Dry area	Dry area We				Wet	open
			I	111	ł		
Winter level	-30/- 80	-5/-10	+10/+5	+10/+ 5	-5/-10	+15/+10	
Summer level	-40/-100	+5/- 5	+15/+5	+20/+10	+5/- 5	+20/+10	

of the old shoot mass took place as early as possible in the spring. In spite of the considerable damage to just-emerging shoots, late burning - i.e. in the second half of April - did not result in significant reduction of the maximal shoot biomass in late July or early August (Mook & Van der Toorn, 1982). In the Wet open I and II and Dry grass plots the reed had been removed by mowing during the summer. In the wet situation the mown areas remained open but in the dry plots the reed was replaced by a grass vegetation. In Dry reed III the stalks had been removed by mowing in wintertime. Irrigation, burning, and mowing were applied from 1972 onward except in Wet open I, which was mown from 1974 onward. Additional information about the treatments can be found in Van der Toorn & Mook (1982).

Unless stated otherwise the present study was performed in stand Dry reed I. Information on the levels of mineral N in 1972 was kindly provided by Van der Toorn and refers to the dry part of the experimental reed field. Data from two other areas, parcel Nz 23 and site 130, were also used. Parcel Nz 23 is a burned dry reed stand situated 2 km east of parcel Nz 17. Soil data were generously put at our disposal by De Glopper. Site 130 (Van Schreven, 1965) is located 6 km north of parcel Nz 17. Sampling took place while Zuidelijk Flevoland was still submerged. Soil data are given in Van Schreven (1963^a).

The steady subsidence of the soil in the IJsselmeer polders (De Glopper, 1973) means that in the course of time the various soil horizons decreased in thickness and depth below the surface. Estimates of the depth and thickness of corresponding soil layers during the 1968-1980 period were based on measurements of subsidence in parcel Nz 23 (De Glopper, unpubl.). For these measurements, marks were inserted in the soil to various depths in August of 1968 and left there. The level of these marks was determined regularly. From these data the rate of subsidence could be calculated.

2.2. Field sampling

The sampling points were distributed over the field in a regular grid with a distance of 5 m between two points.

For sampling of above-ground parts the material of quadrats of 0.25 to 1.00 m^2 was collected (see also Appendix 1). The sampling of the dead above-ground reed mass before and after burning included all above-ground organic material up to the first mineral horizon. All other samplings of above-ground material (shoots for short) included dead parts only which were produced in the current season. To facilitate differentiation between litter of the current season and that of the previous year, for a number of sampling points, netting of 1 m^2 area was placed near the soil surface after burning. The new reed grew through it without being hindered. No measures were taken to include the seed, which was lost from the panicles before the last sampling of the year.

The below-ground biomass was assumed to be equal to the biomass of living rhizomes. In those few cases in which the amount of roots (>1 mm \emptyset) and dead rhizomes was estimated, the total of both fractions was found to be less than 15% (on dry weight base) of living rhizomes. Below 75 cm rhizomes were never found. In 1974 pits of 0.25 m² area were dug to collect the rhizomes. For this purpose soil cores of 9 to 20 cm \emptyset were taken in 1975 (see also Appendix 1).

Soil samples for estimation of chemical constituents and for counting numbers of NH₄⁺-oxidizers were combined from at least five cores, each with a diameter of 2.4 cm.

2.3. Experimental methods

Litter for incubation experiments was collected on 12 July 1975. The samples included the whole litter layer on the mineral soil. Shells and roots were removed. The material collected in "Dry reed I" consisted of litter left after the area had been burned twelve weeks earlier. Litter collected in "Dry reed III" consisted of material that remained after the area had been mown and the stalks had been removed the previous winter. Litter from burned areas (hereafter named "burned") contained 1.63% N, 30% organic carbon and 49% ash on oven dry basis. In litter from the mown fields, these contents were 1,67%, 30%, and 33%, respectively. For incubation the litter was clipped to bits not larger than 1 cm and water was added until the moist material contained 65% water by weight. Jars (1 |) were filled with 75 g portions of the moistened litter and were loosely closed with lids during incubation. Water lost by evaporation was replenished every 10 days. Two series of three jars were prepared of both types of litter. From the jars analysed at t₅, subsamples were taken at t₂. In converting incubation periods of 15, 25, and 30°C to equivalent periods of 9°C it was assumed that the effect of the incubation was only proportional to length of incubation and to a rate constant, reflecting the temperature. Rate constants (k. week-1) were calculated from the temperature (°K) using the equation $\log k = 7.71 - 2758 (1/T)$, given by Stanford et al. (1973). Corresponding Q₁₀ values ranged between 2.0 and 2.2.

Disappearance of N from the litter layer was estimated in "Dry reed I". After burning in 1975, litter was removed from three 0.8 m² quadrats and replaced by an amount of mixed litter equivalent to 180 kg. ha⁻¹ N. Netting was placed over the quadrats to help distinguish new litter. The reed grew through the netting.

To follow the course of mineral N in the soil when the production level of the reed was low, three 30 m² quadrats were kept close-cropped by clipping every 10 days. Soil sampling was restricted to 4 m² in the centre of the quadrats. For each quadrat, one combined sample was prepared. From the surroundings of the quadrats three control samples were collected.

2.4. Analyses

2.4.1. Analyses of reed materials

Total N was estimated by the Kjeldahl method using HgO as catalyst (Steyermark, 1961).

Organic carbon was estimated using the wet digestion procedure of Minderman (1967). CO₂ evolved by boiling in acid without oxidant was subtracted as being carbonate carbon.

Total P was determined colorimetrically by the ammonium molybdate method, after digestion by heating in conc. H_2SO_4 adding conc. H_2O_2 to speed up oxidation.

Insoluble matter is identical with the residue obtained after applying the extraction procedure of Minderman & Bierling (1968). In this procedure extraction (hydrolysis) is performed successively with hot ethanol/benzene (1/1), hot water and hot $0.2N H_2SO_4$, leaving a residue which mainly consists of cellulose and lignin.

Tissue nitrate was estimated with an Orion model 9207 specific-ion electrode. For extraction, 500 mg pulverised plant material was shaken for 30 min with 10 ml of a solution of $AI_2(SO_4)_3$, H_3BO_3 , NH_2SO_3H , and Ag_2SO_4 , brought to pH 3 by adding NaOH (Orion Analytical Methods Guide, 1978). Mineral N in litter was extracted and estimated by the same method as used for soil samples (section 2.4.2.).

Nitrate-reductase activity (NRA) was estimated by an intact-tissue assay (Jaworski, 1971), with the use of 2.5% propanol by volume and 100mM nitrate in the incubation solution. The most recent fully unfolded leaf of each shoot (all shoots collected close to noon) was split along the midrib and cut into 1-cm pieces. During the approximately 2 hours between collection and incubation, the bags containing the leaf material were cooled in ice. Calculation of NRA was based on the production of nitrite at 30°C in the period between 60 and 80 min after the start of incubation. In this period production of nitrite was fairly constant.

2.4.2. Soil analysis

Total N was determined by the Kjeldahl method, with Se and CuSO₄ used as catalysts.

Total carbon was estimated by dry oxidation (analysis by Laboratory for Soil and Crop Testing, Oosterbeek). Organic carbon was calculated from total carbon by subtraction of carbonate carbon estimated by the Scheibler method. Humus was calculated as organic carbon times 100/58.

Mineral N (exchangeable NH⁺₄-N, NO⁻₃-N and NO⁻₂-N) was extracted by shaking 125 g fresh soil (litter) with 300 ml 1N K₂SO₄ for 90 min. NH⁺₄-N was distilled by steam distillation after the filtrate was brought to pH 9.2 with borax (final conc. 0.02M). The distillate was assessed by nesslerization.

 NO_3^-N , including NO_2^-N if any, was reduced to NH_4^+-N in the presence of Devarda alloy. Prior to reduction, NH_4^+-N was removed by boiling for 15 min after the filtrate had been brought to 0.5M relative to NaOH. During the distillation of the boiled mixture in the presence of Devarda alloy, the NaOH concentration increased from 0.8 to 2.2 M. NH_4^+-N released by distillation of the boiled mixture in the absence of Devarda alloy was subtracted.

Fixed NH⁺₄-N was extracted with a mixture of diluted HF and HCl (Bremner, 1959). After neutralisation of the extract with NaOH, NH⁺₄-N was distilled in the presence of borax. Exchangeable NH⁺₄-N was subtracted.

P contents in the soil of parcel Nz 17 and Nz 23 were given by Van der Toorn (unpublished) and De Glopper (unpublished), respectively, and were estimated according to Hofstee (1983).

Most probable numbers of NH⁺₄-oxidizers were determined according to Pochon and Tardieux (1962). Soil suspensions were made in deionized water with a Servall Omnimixer. Extra additions of 9 g CaCO₃, 50 µg H₃BO₃, 50 µg MnSO₄, 25 µg CuSO₄. 25 µg ZnSO₄, 10 µg (NH₄)₆Mo₇O₂₄, 10 µg CoSO₄ and - instead of FeCl₃ - 3.4 mg FeNa(EDTA) were applied per liter culture medium. Since diphenylamine was used as a detection reagent, the presence of both nitrite and nitrate in the medium indicated growth of NH⁺₄-oxidizers. The possible presence of nitrate in the medium - and thus the presence of both NH⁺₄- and NO⁻₂-oxidizers in the soil sample - could be checked by using urea to remove any nitrite from the medium before the diphenylamine reagent was applied.

2.5. Expression of data

All contents are expressed on a 105°C-dry weight basis. For the conversion of contents to amounts on an area basis, use was made of dry bulk weights found for parcel Nz 23. The dry bulk weights of 1968 were calculated directly from the dry matter and humus contents of the water-saturated soil in parcel Nz 23. Dry bulk weights of the years after 1968 were deduced from those of 1968, the subsidence data being used to estimate the decrease in thickness of corresponding soil layers. Results given without the standard error of the mean apply to combination of samples. For soil data on an area basis, variation of dry bulk weight was not included in the standard deviation.

3. Nitrogen economy

3.1. Distribution of nitrogen among shoots and rhizomes

Table 3.1 shows that there is a yearly course in rhizome biomass, i.e. a decrease during the first half of the season and an increase during the second half. However, the differences between the mean biomasses given in the table are generally not significant. More support for differences in biomass is given by the seasonal changes in the soluble matter content of the rhizomes. It is obvious that the course of soluble matter content means that there is transport of assimilated matter from the rhizomes into the shoots and back. It is plausible that the 3.9 t. ha⁻¹ d.m. on June 4 - about five weeks after growth of shoots had started - mainly was produced with the aid of assimilated matter withdrawn from the rhizomes. At that time the leaves hardly were unfolded, so that the production by photosynthesis could not have been important in the foregoing period.

		Biomass (1		N (%)	Soluble matter ** (%)	
1974	3 Aug. 27 Nov.	shoots 13.6 ± 0.6* 10.8 ± 0.7	rhizomes 23.5 ± 1.5 25.0 ± 2.5	shoots 1.77 ± 0.05 1.18 ± 0.05	rhizome 1.21 ± 0 1.45 ± 0	es rhizomes .03 49.4 ± 0.2 .03 54.2 ± 1.1
1975	22 March 4 June 13 Aug. 30 Sept. 7 Nov. 7 Dec.	$0 \\ 3.9 \pm 0.3 \\ 11.1 \pm 0.5 \\ 10.5 \pm 1.1 \\ 9.7 \pm 0.8 \\ 11.3 \pm 0.4$	$22.6 \pm 2.5 \\ 16.9 \pm 1.3 \\ 22.8 \pm 0.9 \\ 31.0 \pm 3.3 \\ n.d. \\ 25.0 \pm 1.3$	n.d. 2.93 ± 0.04 1.79 ± 0.04 1.57 ± 0.05 1.34 ± 0.03 1.31 ± 0.03	$\begin{array}{c} 1.53 \pm 0 \\ 1.42 \pm 0 \\ 1.06 \pm 0 \\ 1.12 \pm 0 \\ \text{n.d.} \\ 1.38 \pm 0 \end{array}$	$\begin{array}{cccc} .02 & 53.6 \pm 0.3 \\ .05 & 47.7 \pm 0.4 \\ .03 & 45.6 \pm 0.1 \\ .04 & 54.1 \pm 0.1 \\ & & & & & \\ & & & & & \\ & & & & & \\ .03 & 56.6 \pm 0.4 \end{array}$

Table 3.1. Standing crop of biomass, N content and soluble matter content of shoots and rhizomes during the period of 3 August 1974 to 7 December 1975

* \pm S_m (standard error of mean).

** % soluble matter = 100% minus % insoluble matter; for determination of insoluble matter replicate samples were mixed to have two different combined samples or only one combined (30 Sept.).
 n.d. no determination.

In 1974 the storage of assimilated matter in the rhizomes after August is accompanied by a decrease of shoot biomass, whereas this is not the case in 1975. An obvious decrease of shoot biomass by the end of the growing season was also found by Chapin et al. (1975) for tundra vegetation. The shoot biomass in August and November 1974 contained 31.4 ± 0.3 and 28.3 ± 1.3 per cent soluble matter, respectively (data not shown). Because of this small and not significant decrease in soluble matter content, it has to be assumed that in 1974 both the soluble and insoluble shoot components (e.g. cellulose) were involved in the decrease of shoot biomass. The possibility, that shoot cellulose is also mobilized to build up carbohydrate reserves in the rhizomes, cannot be excluded as was found by Wiemken-Gehrig et al. (1974) that in an Ipomoea species cellulose of wilting flowers is mobilized and utilized again in new flowers. The absence of a decrease in shoot biomass in 1975 is probably related with the heavy night frost at the end of May as a result of which the greater part of the shoots died off and were replaced by new ones. From a comparison of growth in damaged and undamaged stands in the experimental reed field it can be concluded that this night frost was probably the cause of the lower shoot biomass in August 1975 as compared with 1974 (Mook & Van der Toorn, 1982). The result of the delayed start of the growth in 1975 could have been that a considerable photosynthetic production fell together with storage of assimilated matter in the rhizomes. Therefore, the withdrawal from the shoots could have been compensated.

Another picture of the internal circulation can be obtained from the seasonal course of the N content of shoots and rhizomes. Table 3.1 shows that the N content of the shoots in both years decreases after August, whereas the N content of the rhizomes increases. Also the appearance of the new shoot biomass in the first half of the growing season coincides with a decrease of the N content of the rhizomes.

The amounts of N present in shoots and rhizomes, calculated as kg. ha-1 N, are shown in Figure

3.1. Roughly the picture is the same as is shown in Table 3.1, viz. a decrease of shoot N is coupled with an increase of rhizome N and an increase of shoot N is coupled with a decrease of rhizome N. Because the course of biomass more or less is the same as that of the N content in the same parts of the reed plants, the effects are even more pronounced, at least judging from the amounts of N present per ha by March, August and December. Introduction of the biomass, however, brings a large variation with it.



Figure 3.1. Seasonal course of shoot N (A) and rhizome N (B) levels; vertical bars express \pm S_m

To make an estimation possible of the maximum and minimum amount of N, which circulates yearly between shoots and rhizomes, the net changes in shoot N and rhizome N are calculated in several ways (Table 3.2). With method I the changes are calculated from the results given in Figure 3.1 and thus are based directly on biomass and N content. To eliminate the large variation of the biomass method II and III are applied, which differ from method I in that the calculations are made on the basis of assumed biomasses. With method II it is assumed that the shoot biomass remains unchanged for the rest of the year after August. Shoot biomass of both 1974 and 1975 is fixed at 11.1 t. ha⁻¹ d.m. Rhizome biomass is assumed to remain 22.8 t.ha⁻¹ d.m. throughout the whole observation period. By disregarding the changes in biomass, the calculated changes in kg.ha⁻¹ N will be minima with this method. With method III (only applied for rhizome N) the rhizome biomass of August 1975 is assumed to be 22.8 t.ha⁻¹ d.m. and the biomasses at the other sampling dates are calculated from that by multiplying with a factor, expressing the difference in soluble matter content (see also *Table 3.1 and legend of Table 3.2*). In doing so it is assumed that the amount of insoluble rhizome matter (mainly cellulose) present per ha remains constant throughout the year and that there is only a yearly course in rhizome biomass, because there is a change in soluble matter content. The changes in rhizome N calculated with this method are too low, if also insoluble rhizome components (e.g. cellulose) are mobilized for shoot growth and are replenished from the shoots later on in the season. The possibility of cellulose mobilization in reed has already been mentioned in this paper. No doubt exhaustion of rhizomes will be limited because the basal structure has to remain intact. The calculated changes are too high, if in the first half of the season soluble-rhizome matter is transformed into insoluble rhizome matter and the reverse takes place later on in the season.

i <u></u> i <u></u> _		Net changes in kg.ha ⁻¹ N						
Period		Shoots	Rhizomes					
	1		j	11				
AugDec. 1974	-118 (+ 18)	- 65 (+ 7)	+ 76	+ 55	+ 97			
March-June 1975	+116 (+ 10)	n.d.	-106 (+ 39)	- 24 (+ 12)	- 72 (+ 13)			
March-Aug. 1975	+222 (+ 12)	+197 (+ 4)	-101 (+ 39)	-107 (+ 9)	-166 (+ 9)			
AugDec. 1975	- 78 (+ 15)	- 53 (+ 6)	+ 95	+ 73 (+ 10)	+153 (+ 12)			
OctDec. 1975	(± 16) - 18 (± 15)	- 29 (± 6)	- 7 (± 45)	+ 58 (± 12)	(± 15)			

Table 3.2. Net changes of shoot N and rhizome N during various periods of the growing season

I Calculated from the results given in Figure 3.1.

If For calculation of shoot N and rhizome N at the sampling dates the biomass is assumed to be 11.1 and 22.8 t. ha⁻¹ d.m., respectively. S_m reflects only S_m of N content.

III For calculation of rhizome N biomasses are assumed, which express the soluble matter content. A biomass of 22.8 t. ha^{-1} d,m. was multiplied by 54.4/50.6, 54.4/45.8, 54.4/46.4, 54.4/52.3, 54.4/54.4, 54.4/45.9 and 54.4/43.4 to obtain the assumed biomasses of VIII '74, XII '74, III '75, VI '75, VII' '75, X '75 and XII '75 respectively. S_m reflects only S_m of N content.

() ±1 S_m.

It can be proved with method I (Table 3.2) that the decrease of shoot N after August 1974 is higher than that after August 1975. Clearly this is the result of the decrease of shoot biomass in 1974 (compare method II).

The possibility that the decrease of shoot N is due to leaching was checked in 1975. On two plots the shoots of 0.25 m² were kept bent above a tray during the period 1 October - 7 December. The N content of the collected rainwater was compared with the N content of rainwater from control trays without reed. There were no indications that the bent reed shoots died off sooner than the reed outside the trays. During the first 3 weeks (20 mm precipitation) no leaching of N was found. Leaching of N in the next 4 weeks (78 mm precipitation) amounted to 8 kg. ha⁻¹ N (data not shown). In this period the reed gradually died off. The last week of the observation period (29 mm precipitation) showed no leaching. It can be concluded that the contribution of leaching to the decrease of shoot N is only small.

Carry off by means of the seed could be a second way by which N can disappear from the shoots without a resulting increase of rhizome N. Van der Toorn (1972) established that dissemination can occur from November onwards in stands of common reed in The Netherlands, and that 50% of the seeds have left the panicles before the 1st of February. According to Kvet (1973) the entire panicles of reed contain only 5% of the total shoot N by September. According to Dykyjova & Hradecka

(1976), however, this could be 16%. It was roughly estimated for the shoots of December 1975 (data not shown) that at most 20% of the seed had left the panicles and that altogether at the most 200 kg seed (air-dry propagules) was produced per ha. This amount agrees with the maximum value, which can be calculated from the data on seed production of Bakker & Biewinga (1957), assuming a mean weight of 0.2 mg per seed. The data of these authors are based on a type of reed strongly resembling that of the present study (Van der Toorn, 1979). For seeds, selected on the presence of a *caryopsis*, we found a N content of 3.48% (% air-dry weight), whereas unselected seeds containing 3.09% N. Assuming a N content of 3.48% it follows that 200 kg seed represents 7 kg. ha⁻¹ N. It is not likely that the seed production in 1974 was higher, because the number of panicles per ha was about the same in both years (Van der Toorn, pers. comm.). It is clear that carry off of N by the seed cannot have played a significant role in the decrease of shoot N after August, because the amount of N, expected to be present in the seed per ha, was relatively small.

According to method III (Table 3.2) the increase of rhizome N after August 1975 is considerably higher than the simultaneous decrease of shoot N. A high biomass and thus a high standing stock of rhizome N is calculated from the high soluble matter content in the rhizomes in December. It is possible that the biomass is overestimated in this calculation. With method II (constant biomass), however, the impression is also obtained that the increase of rhizome N exceeds the decrease of shoot N. If the leaching of N by rain (8 kg. ha⁻¹ N) is also taken into account, it can be calculated that during the period of October through December 1975 37 kg. ha⁻¹ N (38-[29-8]) may have been taken up from the soil and stored directly in the rhizomes.

From Table 3.2 it is evident that only half of the about 200 kg. ha⁻¹ N, needed between March and August for shoot growth can be withdrawn from the rhizomes and that consequently the other half has to be supplied by the soil. According to method III about 75% of the N, needed for shoot growth can be supplied by the rhizomes. But according to the same method of calculation a considerable amount of soil N is stored directly in the rhizomes later on in the season. Actually, if in 1975 more N was withdrawn from the rhizomes for shoot growth than had been stored in 1974, this larger withdrawal could be related to the night frost at the end of May 1975 as a result of which by June the greater part of the shoots had to be replaced by new ones.

Studying the nutrient supply of reed growing along the edges of a fish fond, Dykyjova & Hradecka (1976) found a decrease of the N content of the shoots after August, which differently from our results was not accompanied by an increase of the N content of the below-ground parts. An increase of N in the below-ground parts per unit stand area was calculated by these authors from the considerable increase of the below-ground biomass in this period (almost a doubling). Also because a decrease of the N content of the below-ground parts was found between May and August, they suggested the existence of internal recirculation.

Mason & Bryant (1975) also investigated the nutrient content of reed along the edges of a broad. Neither did they find an increase of the N content of the rhizomes accompanying the decrease of shoot N after August. From the rise of the N content of the water in the lake these authors assumed that considerable amounts of N were leached from the ageing reed by rain in autumn. It appeared that such a leaching was negligible in our case in 1975. There are no other reports in the literature that N compounds can be leached from ageing shoots in appreciable amounts just like cations (Tukey, 1970). The insignificance of N leaching from ageing shoots by rain was clearly demonstrated by Morton (1977). This author compared the nutrient content of *Molinia* leaves from plots, shielded from rain from August on with that of leaves from unshielded control plots. In both cases it was found that the N content of the leaves had decreased to about 25% of the content of August by January, with the most spectacular decrease during September and October. In the same period potassium showed only a small decrease in the shielded plots, whereas in the unshielded control plots nearly all potassium disappeared, apparently by leaching.

If the decline in shoot N during the second part of the growing season cannot be explained by leaching, it has to be accepted that shoot N is transported into overwintering growing points near the soil surface and into the below-ground parts. Such a transport mechanism was established unambiguously by Woldendorp (1963) in pot experiments with ¹⁵N-fertilized grass. The observed increase of rhizome N supports the idea of internal downward transport of shoot N in the case of reed. It seemed, however, that the increase of rhizome N by the end of the growing season partly can be caused by direct uptake of soil N. Possibly this takes place after an abnormal high exhaustion earlier in the season. On the other hand it might be possible that the transport of N from shoots into rhizomes is higher than the storage capacity of the below-ground parts. If the storage capacity is

exceeded as could be the case in 1974, it is obvious that the N surplus will be excreted by the roots. Enrichment of the soil with ¹⁵N originating from the grass roots later on in the season was demonstrated by Woldendorp (1963).

The impression is obtained that the decrease of shoot N in 1974 is considerably higher than in 1975, if changes of shoot biomass are taken into account. Considerable differences in the extent of the yearly decrease of shoot N were also found by Clark (1977) in the case of a prairie vegetation dominated by grasses. This author found in field experiments that during a period of 5 years following fertilization with ¹⁵N, the amount of ¹⁵N present in the shoot biomass by October ranged between 46% and 91% of the amount present by August. Likewise Woldendorp (1963) found in pot experiments in one year considerable downward transport of shoot N, whereas in another year such translocation was not found at all.

On the basis of Table 3.2 the amount of N, yearly transported from the ageing shoots into the rhizomes and from there into the shoots of the next year, roughly can be estimated to be from 50 to 100 kg. ha⁻¹ N. So with an above-ground incorporation of 200 kg. ha⁻¹ N at the midst of the growing season, the percentage of internal N recirculation would range between 25% and 50%. According to the data of Dykyjova & Hradecka (1976) on shoots and below-ground parts of reed during one growing season, the percentage would be about 50%. On the basis of a 5 year observation period Clark (1977) states a mean of 33% for prairie vegetation. From one year observations Chapin et al. (1975) states 40% for tundra vegetation and Morton (1977) 75% for *Molinia* vegetation. These authors all base the percentages of internal N recirculation on a decrease of above-ground N and do not report on observations concerning possible simultaneous N increase in the overwintering live plant parts.

3.2. Loss of nitrogen due to burning

Charred remnants of plant material still contain N. With complete burning of plant material all N is volatilized, mainly as N_2 and to a small extent also as ammonia and N-oxides (Evans & Allen, 1971). With burning in early spring the dead shoot mass of the reed stand never was completely burnt. The erect stalks were burnt off entirely, whereas the leaf litter was burnt only partially.

Table 3.3 shows the amount of N present in the total dead above-ground reed mass some weeks before and a few days after burning. The difference is regarded as loss caused by burning. Possible N loss, due to leaching during the period of some weeks between the two sampling dates, is included incorrectly. Such a loss is probably inconsiderable, because during December, January and February prior to this period in 1975 there was no significant loss of N. The amount of $(130 \pm 9 \text{ kg. ha}^{-1} \text{ N})$ present in the current year's biomass at 27 November 1974 according to figure 3.1 roughly agrees with the 133 \pm 15 kg. ha⁻¹ N (260 minus 127) brought back above ground in the period between burning of 1974 and of 1975 according to Table 3.3.

Year	Kg.ha ⁻¹ N in dead above-ground reed mass						
	Before burning	After burning	Loss				
1974	$234 \pm 7^{1)}$	127 ± 11	107 ± 13				
1975	260 ± 10	189 ± 8	71 ± 13				

Table 3.3. Loss of nitrogen due to burning of reed vegetation in early spring

Burning: 11 April 1974 and 22 April 1975.

Sampling: 14 March 1974, 12 April 1974, 4 March 1975 and 24 April 1975. 1) \pm S_m.

It is evident that, considering the N need of a highly productive vegetation as is the reed vegetation under study, a yearly loss of about 90 kg. ha⁻¹ N is considerable.

According to Grant (1963) about 2 tons of burnable litter can be found per ha in early spring in a *Molinia*-dominant vegetation. Using the data of Morton (1977) it can be calculated that these 2 tons

Table 3.4. Numbers of NH⁴-oxidizers in various soil layers and the levels of nitrate-reductase activity (NRA) and nitrate in the shoots in reed stands with different water levels; the results refer to 1978

Soil sample site and water level		NH ⁺ ₄ -oxidizers (10 ³ cells per g)			NRA ¹⁾ (μM.g ⁻¹ .h ⁻¹ NO ₂)			Nitrate ²⁾ (µM.g⁻¹ NO₃)
	17 July			13 July	15 July	19 July	13 July	
	0-20 cm	60-80 cm	150-170 cm	225-245 cm				
Dry reed II -60 cm	≥34 (≥33) ³⁾	28 (≥54)	14 (≥65)	8 (8)	2.6±0.4	6.5±0.8	3.1±0.3	10.4±1.7
Wet reed I - 5 cm	≥41 (≥42)	24 (13)	8 (4)	2 (8)	1.4±0.3	3.2±0.3	2.6±0.3	4.4±0.9
		20	Oct.			21 Sept.		21 Sept.
	0-20 cm	20-1	00 cm	100-200 cm				
Wet reed +5(-5)cm ⁴⁾	2040 (409)	(7	44 77)	64 (40)		3.4±0.4		0.5±0.2
Wet reed II +10(+10)cm ⁴⁾	350 (478)		44 19)	1 (2)		1.2±0.2		0.2±0.1

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¹⁾ n = 10; values for 15 July refer to samples taken at night.

²⁾ n = 8.

³⁾ Numbers between parentheses refer to duplicate soil samples.
 ⁴⁾ Water level on 21 September given between parentheses.

of litter contain about 10 kg N, which roughly equals the yearly N input to be expected from precipitation. According to the data of both authors, it can be stated that in a yearly burnt *Molinia* vegetation the N supplying capacity of the soil is not charged. For in the latter case there is a low above-ground N need - estimated at 40 kg. ha⁻¹ N (10x100/25) - and a high percentage internal N recirculation (75%). Based on practical experience, it is generally accepted in nature management that the productivity of a *Molinia*-dominant vegetation is not decreased by frequent burning. The fact that a considerable amount of N is incorporated in the shoots by August and that the recirculated amount of N is limited, implies a potentially considerable N loss, if the old reed is burned in early spring. The mean loss of 1974 and 1975 appeared to be 90 kg. ha⁻¹ N. So differently from what happens in the *Molinia* vegetation, the N supplying capacity of the soil is charged considerably by burning the reed yearly.

3.3. Numbers of ammonium-oxidizers in the soil and nitrate-oxidase activity of the shoots

Substantial numbers of NH⁴₄-oxidizers were found, not only above but also below the ground-water *level* (Table 3.4). The permanently water-saturated soil layers (below 100 cm and 10 cm in the Dry reed II and Wet reed I plots, respectively; see Table 2.1), also contained NH⁴₄-oxidizers, but in lower numbers than were found in the upper layers. All samples taken on 17 July contained both NH⁴₄- and NO²₂-oxidizers (data not shown). No other samples were checked for the presence of NO²₂- oxidizers. When the numbers referring to both sampling dates are considered separately, they show a tendency to be higher when the water levels are lower. These higher numbers were accompanied by higher levels of both NRA and nitrate in the shoots. The relationship between water level and nitrate content of the shoots is also shown clearly by Table 3.5. The nitrate content of the shoots was higher in fields with lower water levels during the period before sampling. Indirect aeration of the soil by leakage of O₂ from the roots, which were observed down to 2.3 m depth, is evidently a less effective oxygen supply, resulting in lower numbers of NH⁴₄-oxidizers. From the coupling between the NRA level and NH⁴₄-oxidizer population actually oxidized NH⁴₄-N.

Table 3.5. Nitrate content in shoots of reed in stands differing as to water levels; the results refer to 1974

Sampling site	Water variation (cm)	Shoot nitrate (μM.g ⁻¹ NO ₃)		
	22 April-6 Aug.	8 July	6 Aug.	
Dry reed I	-40/-70	7.2 ±1.8 (n=2)	· 4.3±1.3 (n=5)	
Wet reed I	0/0	3.7±0.6 (n=4)	2.7±0.3 (n=4)	
Wet reed III	+15/+15	0.7±0.4 (n=4)	1.6±0.3 (n=4)	

Fertilization with large amounts of nitrate applied before the shoots were fully grown did not lead to a spectacular increase of NRA, as concluded from the results of an experiment performed in a dry reed field during July of 1980 (data not shown). In this experiment, during a three-week period with 77 mm precipitation during the first two weeks, 300 kg ha⁻¹ N was applied by spraying the soil with a Ca(NO₃)₂ solution, which gave 160 and 110 kg. ha⁻¹ NO₃-N in the 0-20 cm and the 20-60 cm layers, respectively, at the end of the three weeks. In the absence of fertilization, nitrate levels were negligible. NRA levels in the leaves of the fertilized and unfertilized reed at the end of the three-week period were 2.4 ± 0.2 and 1.6 ± 0.3 μ M. g⁻¹ NO₂, respectively (n = 8), and the corresponding nitrate contents of the leaves were 22.7 and 13.9 μ M.g⁻¹ NO₃. During the first and second weeks

of the experiment NRA was higher (up to 7 μ M.g⁻¹.h⁻¹ NO₂). No significant differences, however, were found between the two types of trial. It may be concluded from this experiment that the uptake capacity of the reed is not adapted to large amounts of nitrate in the soil.

Nitrifiers were also found in water-saturated soil layers in places where reed growth had ceased about five years earlier (Table 3.6). The numbers were high, but lower than in the neighbouring sites with reed. Because growth of the isolates was suppressed by N-serve (see legend to Table 3.6), the nitrifiers must have been autotrophic NH⁴₄-oxidizers (Shattuck & Alexander, 1963), which need oxygen for growth. Therefore, the only explanation for the presence of these organisms in the permanently water-saturated soil layers of the sites without reed is that about five years earlier, when the whole area was overgrown with reed, leakage of air from invading roots enabled NH⁴₄-oxidizers to become established and that these NH⁴₄oxidizers survived under the anoxic conditions for several years after the roots had died off.

Reed	stands	Sites without reed			
Sampling site and water level	NH ⁺ -oxidizers (10 ³ cells.g ⁻¹)	Sampling site and water level	NH ⁺ -oxidizers (10 ³ cells.g ⁻¹)		
Dry reed I	37	Dry grass	6		
-100 cm	(38) ¹⁾	-100 cm	(8)		
Wet reed I	64 ²⁾	Wet open I	7		
+5 cm	(40)	+5 cm	(6)		
Wet reed II ³⁾	0.7	Wet open II ³⁾	0.7		
+5 cm	(0.7)	+10 cm	(0.1)		

Table 3.6. Numbers of NH⁺₄-oxidizers in the 100-200 cm soil layer of various reed stands and of neighbouring sites without reed; the results refer to 20 October 1978

1) Numbers between parentheses refer to duplicate soil samples.

2) Values for Wet reed I taken from Table 3.4.

 At these sites soil samples were taken from the 145-155 cm layer on 17 November 1979. When 10 or 1 ppm N-serve (Dow Chemical Company) was added to the medium, these soil samples showed no growth of NH⁺₄-oxidizers for two weeks.

Since survival of NH₄⁺-oxidizers under anoxic conditions can also be expected in the permanently water-saturated.soil layers of the reed sites, high numbers of nitrifiers in these layers do not necessarily reflect a high nitrification rate. On the basis of 1 mg NH₄⁺-N for the synthesis of 2 x 10⁸ NH₄⁺-oxidizer cells (Alexander, 1960), not more than 2.5 kg. ha⁻¹ NH₄⁺-N would be required for the synthesis of 10^5 NH₄⁺-oxidizers.g⁻¹ in the 100-200 cm soil layer of a reed field. In the steady state, populations of NH₄⁺-oxidizers can convert very large amounts of NH₄⁺-N. After applying 28 kg. ha⁻¹.d⁻¹ NH₄⁺-N by irrigation on a fallow field plot with 10^4 NH₄⁺-oxidizers.g⁻¹ in the upper 2.5 cm of the soil, Ardakani et al. (1974) found a steady-state conversion rate of 14 kg. ha⁻¹.d⁻¹ NH₄⁺-N. It is clear that such a high conversion rate in the root-containing water-saturated soil of our reed fields, which contained large amounts of NH₄⁺-N (section 3.5), considerably more nitrate would have been produced than could be taken up by the reed. Consequently, large amounts of mineral N would have disappeared by denitrification.

The tendency for higher numbers of NH⁴₄-oxidizers to occur, when the water tables were lower was accompanied by higher leaf-NRA levels. This suggests that part of the N was taken up as nitrate. Strong correlations between NH⁴₄-oxidizer numbers and leaf-NRA levels were found by Smit & Woldendorp (1981), who estimated NH⁴₄-oxidizer numbers of the rhizosphere of *Plantago* species. The range of reed-leaf NRA (1-7 μ M.g⁻¹.h⁻¹ NO₃) equals that of *Hypochaeris* species (Van de Dijk, 1980) and *Plantago* species (Smit & Woldendorp, 1981). In *Urtica dioica* (Hofstra, pers. comm.), soybean (Jaworski, 1971), and dwarf bean (Breteler et al., 1979), levels of 30, 40, and 50 μ M.g⁻¹.h⁻¹.

 NO_2^- leaf NRA, respectively, were found with the same method as was used in this study. Thus, it is evident that reed belongs to a group of species with a limited capacity for nitrate assimilation per unit of shoot biomass.

Numbers of NH⁴₄-oxidizers were of the same order of magnitude as those occurring in the top layer of fertile calcareous soils (Van Schreven & Harmsen, 1968; Van Schreven & Sieben, 1972), and considerably higher than the numbers in productive grassland soil (Meiklejohn, 1968). Such numbers are more than sufficient to bring about a nitrate production large enough to meet the whole N requirement of the reed. As will be shown in section 3.6 the major part of the mineral N was taken up from the residual NH⁴₄-N stock in the unripened and permanently water-saturated soil layers. Thus, if nitrate were the main N source for the reed, nitrification would be concentrated in an anaerobic environment with air leakage from the roots as the sole source of oxygen. This type of nitrification was, however, of limited significance, notwithstanding the high numbers of NH⁴₄-oxidizers in the anaerobic soil layers. This was included from the lower NRA and nitrate levels in the shoots when the water table was high.

3.4. Mineralization of litter after burning

3.4.1. Accumulation of mineral nitrogen upon incubation of litter

Mineralization of litter from "burned" was considerably slower than that of litter from "mown" (Fig. 3.2). Both materials had a C/N-ratio of about 18. The mineral N produced in both cases was made up of more than 90% nitrate N. In both types of litter the pH ranged between 7.0 and 7.3 during incubation. Heat sterilization of the whole litter layer was not a plausible cause for the slower mineralization of the litter from burned, because heat penetration during vegetation fires is limited to the top few centimetres of the profile (Raison & McGarity, 1980). After burning the litter layer was still at least 5 cm thick. As the litter was collected twelve weeks after burning, there should have been a significant replacement of the microbes that have been killed. The lower mineralization of the *burned litter could* be the result of heat sterilization, or due to the formation, during burning, of toxic (Raison & McGarity, 1980) or other compounds that do not decompose easily, or the coal dust, that was mixed thoroughly with the saved leaf and stem parts, before filling the jars, had an inhibitive effect.



Figure 3.2. Cumulative percentage of organic nitrogen mineralized on incubation of litter remaining in reed stands, in which yearly removal of dead shoot mass took place by burning an by mowing. At t₀, t₁, t₂ and t₅ litter from "burned" contained 361 ± 1, 246 ± 48, 396 ± 58 and 1050 ± 120 ppm mineral N, respectively. In litter from "mown" these values were 342 ± 1, 759 ± 9, 1840 ± 10 and 3450 ± 10 ppm. Before continuing incubation at t₂ litter was dried at room temperature until air dry and remoistened. At t₄ litter was kept at -15°C for 24 hours.

To facilitate estimation of mineralization under field conditions mineral N production rates (Fig. 3.2) were expressed as rates at a mean soil temperature of 9°C. Based on the mineralization rate between t_2 and t_5 (Fig. 3.2) 7% of the organic N in litter from "burned" will have been mineralized after one year at a mean temperature of 9°C. The lag phase between t_0 and t_1 has been neglected with this calculation. It has also been assumed that the varying temperature, the drying and the freezing between t_2 and t_5 (see legend of Fig. 3.2) have roughly the same stimulating effect on mineralization as do the natural changes in soil conditions.

3.4.2. Disappearance of nitrogen from the litter layer after burning

Disappearance of litter N between the burnings of 1975 and 1976 was measured in a field experiment. After the 1975 burning there was 180 kg. ha⁻¹ N present in the partly burned litter, which was reapplied on a cleared mineral soil. Before the 1976 burning $21 \pm 4\%$ of the N in the reapplied litter disappeared (data not shown).

Disappearance of litter N, during the period 1968-1975, was estimated from the amount of N incorporated in the above-ground production, the losses of N due to burnings and the amount present after burning in 1975. From 1970 onwards the above-ground production of reed was fairly constant (Mook & Van der Toorn, 1982). The 1969 production was about one third of that of 1970 and after, whereas the 1968 production was negligible (Van der Toorn, pers. comm.). It is plausible that in the spring 1972, when the reed was burned for the first time, not only material produced in 1971 but material produced in 1969 and in 1970 was also burned, because shells became visible on the burned litter layer (Van der Toorn, pers. comm.).

In a growing season 140 kg. ha-1 N was produced in the shoot mass and the loss by burning was 90 kg, ha⁻¹.y⁻¹ (Section 3.2). Thus litter N increased by 50 kg. ha⁻¹.y⁻¹ N. Assuming that the same efficiency of burning occurred during the period 1972-1975, 267 kg.ha⁻¹ N could be expected in the litter layer after burning of 1975 (Appendix 2). As the litter layer contained 190 kg.ha⁻¹ N after burning in 1975 (Section 3.2) instead of 267 kg, 29% of the litter N, not lost by burning, had disappeared. Thus, with an increase of 50 kg.ha⁻¹.y⁻¹ litter not lost by burning, 14.5 kg. ha⁻¹.y⁻¹ N disappeared, or 9% of the average amount of 160 kg. ha⁻¹ N present in the litter layer after the burnings of 1974 and 1975 (Section 3.2). This 9% disappearance of N is considerably lower than the 21% found in the field experiment in the period between the burnings of 1975 and 1976. A higher disappearance rate in the field experiment could be a result of mixing the litter material before it was applied. If the disappearance of N from the litter layer was assumed to be by mineralization, this was probably an overestimation, because organic matter could have moved into the mineral soil. The mineralization rate from the incubation experiment (Section 3.4.1) could also be an underestimation, because leaching of inhibitive components could not occur. The litter incubation in the laboratory showed that at least 7% of the N present in the litter layer was mineralized in one year. In the litter decomposition experiment in the field 21 ± 4% N at the most was mineralized. Based on the accumulation of litter N in the period 1968-1975 at the most 9% was mineralized. Thus an average of 11% Nmineralization per year is probably not far removed from the real rate. With an average amount of 160 kg. ha⁻¹ N present in the litter layer in 1974 and 1975, this corresponds to a mineralization rate of about 20 kg. ha⁻¹.y⁻¹ N.

3.5. The stock of nitrogen (mineral and organic)

In the absence of repression of reed growth by close-cropping, mineral N decreased by 41 kg. ha^{-1} N in the 0-100 cm layer during the 1975 growing season (Table 3.7). Under the close-cropped conditions there was no such decrease. It therefore seems plausible that the decrease was due to the extra production by the untreated reed. At the start of the experiment, 20% of the mineral N consisted of NO₃⁻-N whereas at the end this was 40 and 70%, in the untreated and close-cropped situations respectively. At about 600 kg. ha^{-1} N, the 100-200 cm layer contained a considerable amount of mineral N consisting mainly of NH₄⁺-N. The NO₃⁻-N level was less than 1 ppm (4.5 kg. ha^{-1}). There was no significant change in the amount of mineral N in this layer during the growing season.

Table 3.7. Seasonal course of mineral N levels for locations where reed was kept close-cropped between 14 May and 6 October 1975 and for untreated neighbouring sites

Date	Depth of	Mineral N in kg.ha ⁻¹			
of sampling	soil layer (cm)	Close-cropped reed	Untreated reed		
14 May	0-100 100-200	62 ± 5 561 ± 83	64 ± 3 607 ± 18		
2 July	0-100 100-200	59 ± 8 722 ± 28	40 ± 3 607 ± 87		
6 Oct.	0-100 100-200	72 ± 8 603 ± 41	$\begin{array}{rrr} 23 \pm & 3 \\ 580 \pm 60 \end{array}$		

In addition to exchangeable NH^{*}₄-N, fixed NH^{*}₄-N can be expected in a clay soil. The large differences between upper and lower soil layers with respect to the content of exchangeable mineral N are not reflected in the values for fixed NH $_{4}^{+}$ -N (Table 3.8). Before emergence in 1968 there were also considerable amounts of exchangeable mineral N in the upper soil layers (Van Schreven, 1963^a). It is clear that the disappearance of this N was predominantly due to the development of the reed vegetation. If uptake of fixed NH⁺₄-N had occurred between 1968 and 1975, the content of fixed NH₄-N would have been lower in the 0-100 cm than in the 100-150 cm layer, unless the two layers differed in fixing capacity and thus in their content of fixed NH₄⁺-N in 1968. The capacity to fix NH₄⁺⁻ N depends on the chemical constituents of the clay and the particle size (Nommik, 1965). The three chief components of the $< 2-\mu$ fraction, i.e., kaolinite, illite, and montmorillonite, were present in the same proportions in all three layers (Van der Plas & Van Doesburg, pers. comm.). The 0-100 and the 100-150 cm layers were roughly similar with respect to particle size (Table 3.8) and thus also with respect to fixing capacity. In view of the similar fixed NH₄-N contents (by weight) in 1975 and the similar fixing capacity of the two layers, it can be concluded that fixed NH⁺₄-N did not decrease significantly during the 1968-1975 period. Considering the large particle size of the 150-200 cm layer, the lower fixed NH⁴-N content of this layer is consistent with the negative correlation between fixed NH₄⁺-N and particle size found for IJsselmeer soils (Van Schreven, 1963^a).

Soil	Exchangeable mineral N ¹⁾ (ppm) (kg.ha ⁻¹)		Fixed NH¼-N (ppm) (kg.ha ⁻¹)		Particle size ²⁾		
layer					 >50μ	2-50µ	 <2μ
(cm)					(% by weight)		
0-100 100-150	3 85	23 187	240 250	1850 560	2.5 1.4	79.6 77.2	17.9 21.4
150-200	174	392	200	450	21.0	62.1	16.9

Table 3.8. Exchangeable mineral N, fixed NH⁺₄-N, and particle-size composition of various soil layers on 6 October 1975

1) Including NO₃-N.

2) Kindly determined by Department of Soil Science, Agriculture University, Wageningen.

The humus contents of the 0-100 and 100-200 cm layers were about 7 and 14%, respectively (data not shown), and the corresponding C/N ratios of the humus were 14 and 16. From the rather high humus contents and low C/N ratios, significant net mineralization of N could be expected especially in the ripened upper 70 cm of the soil, because conditions changed in this layer after the long period of water saturation. Such mineralization would be reflected in an increase of mineral N in the 0-100 cm layer of the plots in which reed growth was suppressed by close-cropping. During the 1975 growing season, however, no clear increase of mineral N was found in these plots (Table 3.7). It is possible that under the close-cropped conditions mineralized N, if any, was taken up by the shoots, which were removed every 10 days. Over the whole experimental period, 2.5 t.ha⁻¹ shoots, corresponding to 90 kg. ha⁻¹ N, were removed. However, because the shoots were very young, at least half of the required N had probably been withdrawn from the rhizomes instead of from the soil (Section 3.1). Thus, if the requirements of the close-cropped reed for below-ground production were nealigible. not more than about 50 kg. ha⁻¹ mineral N was supplied by mineralization in the 0-100 cm layer. As fixed NH₄-N did not decrease significantly during the 1968-1975 period, it was an N source of minor importance. The upper 2 m of the soil contained enough exchangeable mineral N to meet the requirements of fire-managed reed growth for at least three seasons. The level of mineralization in the 0-100 cm layer, 50 kg. ha⁻¹.y⁻¹ N, was considerably lower than on fallow plots in Oostelijk Flevoland, on which a mean increase of 150 kg. ha⁻¹ mineral N was found for the 0-100 cm layer during nine-month periods (De Jong, pers. comm.). The fallow plots were cultivated with annual crops and N-fertilized for several years, which might explain the higher level of mineralization.

3.6. Losses of nitrogen from 1968 through 1975

Losses of N were roughly estimated by comparing the amounts that disappeared from the soil with those stored in the living and dead reed mass from 1968 onward. For this purpose, data of two areas had to be added to the data on mineral N in parcel Nz 17 (Table 3.9). Mineral N contents of site 130 were considered as the contents of the study area in 1968. For total N, data of parcel Nz 23 were used. The soil profile of the study area corresponded roughly with that of site 130 and parcel Nz 23 (Ente, 1963). It was assumed that the three areas were approximately comparable with respect to changes in amounts of mineral and total soil N as well as the uptake of N by the reed.

	Layer I		Layer II			
	Depth ¹⁾ (cm)	Min. N ²⁾ (kg	Total N .ha ⁻¹)	Depth ¹⁾ (cm)	Min. N ²⁾ Tota (kg.ha ⁻¹)	
Aug. 1968	0.63	488	7860	63-123	547	9890
May 1972	0-52	31	n.ď.	52-107	118	n.d.
Dec. 1975	0-50	12	7730	50-100	12	9430

Table 3.9. Course of mineral and total soil N levels between 1968 and 1975

Due to subsidence, the depth and thickness of layers 1 and II decreased from 1968 onward.
 Except for layer I by May 1972 and December 1975 negligible amounts of nitrate N occurred.
 n.d. no determination.

The uptake figures used in the budgets (Table 3.10) were based on the amounts of N present in shoots, litter, rhizomes, and roots (> 1 mm ø) in May 1972 and December 1975 (Sections 3.1 and 3.2: Mook & Van der Toorn, 1982; and pers, comm.). The uptake includes the losses due to burning. N from precipitation was included as completely available and assumed to be 15 kg. ha⁻¹,y⁻¹ N (Henkens, 1976). The supply was not explained by mineralization where it could be explained by a decrease of mineral N. It was assumed that uptake from upper layers predominated over uptake from deeper layers. Thus, the whole decrease of total N in layer I (Table 3.9) and the major part of the decrease in layer II were ascribed to uptake of mineral N in the 1968-1972 period. Mineral N decreased more than total N did (Table 3.9). The extra decrease of mineral N has been ascribed to immobilization. This immobilization can be explained as due to accumulation of fine root material, because the organic matter content of the soil increased significantly. In layers I and II of parcel Nz 23, organic matter increased by 17 and 11 t.ha⁻¹, respectively, during the 1968-1975 period. The immobilization calculated for layer I in the first of the two periods is improbably high. The amount of mineral N in layer 1 in 1968 (Table 3.9) may have been overestimated. By August in 1968, the upper dm of the soil of Nz 23 was already aerated. Thus there might have been losses from the topsoil during the drainage before August 1968, e.g. by volatilization of ammonia. Such losses were included in the figure for total N but not in that for mineral N, because the latter refers to a situation several years before emergence (Van Schreven, 1963^a).

Period		1968-1972		1972-1975
Taken up by reed	668		552	
Supplied by: precipitation	60		53	
layer l	130	(7860-7730) ¹⁾	0	
layer II	398	(9890-9430-62)	62	(522-53-0-407)
deeper layers	80		407	
Immobilized in: layer I	327	(488-31-130)	19	(31-12)
layer II	31	(547-118-398)	44	(118-12-62)
Total immobilization	358	(327+31)	63	(19+44)
Lost	100	. ,	0	•

Table 3.10. Tentative N budgets	for the 1968-1972 and	1972-1975 periods;	amounts are given in
kg. ha ⁻¹ N			-

1) Values between parentheses were calculated with data shown in Table 3.9 and this table.

If the accumulated soil organic matter was fine root material, which would contain 1.3% N, the amount of mineral N immobilized during the 1972-1975 period was not sufficient to explain the accumulation of 10 and 7 t.ha⁻¹ organic matter in layer I and II respectively. Mineralization of original humus at a rate of about 50 kg. ha⁻¹.y⁻¹ N might have supplied the required amount (calculation not shown).

The tentative budgets indicate that in the 1968-1972 period the N-requirements of the reed were largely met by N supplied by precipitation and present in the two upper soil layers, and that during the 1972-1975 period the major part of the N was taken up from deeper layers. No mineralization was necessary to meet the requirements of the reed. The probability of a supply by the deeper layers will become clear in the next two sections, in which the losses are discussed.

3.6.1. Losses in the 1968-1972 period

It seems likely that anaerobic mineralization in the permanently water-saturated deeper soil layers, i.e. below layer II (Table 3.9), was no longer significant, since it concerned what are called Almere sediments, which were formed during the first 1600 years of our era (De Glopper, 1973 and unpubl.). Thus, losses of N equal disappearance of mineral N from the soil below layer II minus the uptake of N from that part of the soil. The losses may have been overestimated due to the neglect of possible immobilization of mineral N.

About 180 kg. ha⁻¹ mineral N was calculated to have disappeared from the soil below layer II during the 1968-1972 period (Appendix 3). In this calculation the contents of mineral N (by weight) below a depth of 150 cm in 1968, were estimated by extrapolation from the contents in the layers between 20 and 150 cm, which increased asymptotically with depth (Van Schreven, 1963^a). The disappearance of 80 of the 180 kg. ha⁻¹ mineral N can be explained by the requirements of the reed (Table 3.10). Thus, 100 kg. ha⁻¹ N was lost in the 1968-1972 period. This loss represents a maximum amount lost by denitrification. Possible losses due to carry-off of seeds, especially seeds of *Senecio tubicaulis* in 1968 and 1969, and losses caused by draining after August 1968, are included.

3.6.2. Losses in the 1972-1975 period

Assessment of the losses in the 1972-1975 period requires estimation of the disappearance of mineral N from the soil between layer II and the pleistocene sand. Disappearance of mineral N from the soil between layer II and the 200-cm level was calculated to be 287 kg. ha⁻¹ mineral N (Appendix 4). Disappearance below a depth of 200 cm was estimated by extrapolation. In 1975, the 50-100 cm, 100-150 cm, and 150-200 cm layers contained 12, 176, and 404 kg. ha⁻¹ mineral N, respectively. In 1968, the corresponding layers contained 547, 471, and 547 kg. ha⁻¹ mineral N. Thus, between 1968 and 1975 mineral N in these layers decreased by 535, 295, and 143 kg. ha⁻¹, respectively. Calculation based on the conclusion that the amount of disappearing mineral N decreased by a

factor of two for each successive 50-cm depth, showed that 120 kg. ha⁻¹ mineral N disappeared from the soil between 200 cm and the pleistocene sand at 330 cm. Because disappearance from the corresponding layers in the 1968-1972 period can be neglected (Appendix 3), all 120 kg must have disappeared in the 1972-1975 period. This means that the total disappearance from the soil between layer II and the pleistocene sand at 62 kg. ha⁻¹ N, as was done for the budgets shown in Table 3.10, the soil below layer II must have supplied 407 kg. ha⁻¹ N. Since an equal amount had disappeared, there were no N losses during the 1972-1975 period. The basic data in Table 3.10 also permit combinations of lower losses in the first period with the occurrence of losses in the second period or higher first-period losses than postulated combined with the absence of losses in the second period. However, all of these combinations proved to be less compatible with the assumptions made.

4. Phosphorus economy

4.1. Distribution of phosphorus among shoots and rhizomes

The P content of the shoots decreased from August onward, whereas that of the rhizomes increased (Table 4.1). Shoot production until August was accompanied by a decrease of the P content of the rhizomes. The courses of shoot and rhizome P on an area basis (Fig. 4.1) indicate that uptake of P in the shoots until August was coupled with a decrease of rhizome P and that the decrease of shoot P from August onward was coupled with an increase of rhizome P.

Sampling date		P (% dry weight) Shoots	Rhizomes
1974	3 August 27 November	$\begin{array}{c} 0.155 \pm 0.007^{1)} \\ 0.073 \pm 0.002 \end{array}$	0.165 ± 0.004 0.183 ± 0.008
1975	24 March 4 June 13 August 30 September 7 November 7 December	n.d. 0.282 ± 0.004 0.151 ± 0.004 0.124 ± 0.005 0.101 ± 0.003 0.085 ± 0.002	$\begin{array}{c} 0.201 \pm 0.006 \\ 0.196 \pm 0.007 \\ 0.166 \pm 0.004 \\ 0.178 \pm 0.006 \\ \text{n.d.} \\ 0.198 \pm 0.005 \end{array}$

Table 4.1.	Phosphorus	content of	shoots	and	rhizomes	during	the	period	between	3 August	: 1974
	and 7 Decer	nber 1975									

n.d. no determination.

1) S_m

For the calculation of changes in the amounts of shoot and rhizome P use was made of two and three methods, respectively (Table 4.2), because the mean biomass found on the sampling dates showed relatively standard deviations (Section 3.1). With method I, the changes were calculated on the basis of the standing stocks of shoot and rhizome P given in Fig. 4.1 which include the high standard deviations of the biomasses. With method II constant biomasses i.e. those of August 1975, were used to compute the standing stocks of P, on which the estimation of the changes was based. Because the seasonal course of the P content of the rhizomes was roughly the same as the course of the rhizome biomass, changes in rhizome P were probably underestimated by method II. Moreover, the decrease of shoot P during the period between August and December in 1974 is probably underestimated if the decrease in biomass is neglected. With method III it was assumed that the rhizome-biomass value for August 1975 - which showed relatively little variation and differed little from the corresponding figure for 1974 - reflected the real biomass on that sampling date. For the calculation of the other rhizome biomasses, it was assumed that they differed from that of August 1975 only by the content of soluble components, i.e. substances extractable by hot ethanol/benzene, hot water and hot 0.2N H₂SO₄ successively (Section 3.1). Method III would also have led to underestimation of the changes if the insoluble rhizome fraction, consisting mainly of cellulose and lignin, had served as reserve material in addition to the soluble fraction, but this is not plausible, because the soluble fraction consisting mainly of sugars and starch was far from being exhausted during shoot growth until August.

According to method I, rhizome P decreased more in the March-June period than in the March-August period. This means that storage of P occurred during the second half of the latter period, when the shoots still required P. The changes in the corresponding periods found according to method III are more realistic, since this method indicated a gradual decrease of rhizome P during the March-August period. According to method I, the increase of rhizome P in the August-September period was about twice that in the August-December period. This means that an unlikely decrease occurred during the second half of the latter period. The gradual increase of rhizome P indicated by method III is more plausible, because it corresponds with a gradual decrease of shoot P during the August-December period. No explanation can be offered as to why, in most of the cases, method III gave stronger changes than methods I and II did.



Figure 4.1. Seasonal course of shoot P (A) and rhizome P (B) levels; vertical bars express ± S_m.

For a rough quantification of internal P recirculation only the changes over the longer periods (March-August and August-December) were taken into account, because the data for these periods were probably the most reliable. About 20 kg. ha^{-1} P appeared as shoot P during the March-August period (Fig. 4.1). Pooling of the 1974 and 1975 values obtained with the two (three) methods of calculation (Table 4.2) showed that about 10 kg. ha^{-1} P was withdrawn from the rhizomes in the March-August period, whereas during the August-December period 10 kg. ha^{-1} P was withdrawn from the shoots and 9 kg. ha^{-1} P stored in the rhizomes.

Table 4.2. Net changes in the levels of shoot and rhizome P during various periods of the growing season, as estimated by three calculations (I, II, III), with which the original biomasses, assumed constant biomasses, and assumed biomasses reflecting the seasonal course of the soluble matter content were used, respectively

	Net changes	in P (kg.ha ⁻¹))				
	Sho	pots		Rhizomes			
Period					111		
August - December 1974	-13.5 (± 1.4)*	- 9.1 (± 0.7)	+ 7.1 (± 6.1)	+ 4.1 (± 2.0)	+ 9.2 (± 2.4)		
March - June 1975	+11.1 (± 0.9)	n.d.	-12.7 (± 5.6)	- 1.1 (± 2.2)	(± 2.5)		
March - August 1975	+18.6 (± 0.8)	+16.8 (± 0.4)	- 7.4 (± 5.6)	- 8.0 (± 1.7)	-15.9 (± 1.9)		
August - September 1975	- 5.7 (± 1.7)	-3.0 (±0.7)	(± 6.4)	+ 2.8	+10.3 (± 1.9)		
August - December 1975	- 9.1 (± 1.0)	- 7.4 (± 0.4)	+10.7 (± 4.5)	+ 7.3 (± 1.5)	+18.8 (± 1.7)		

* Values between parentheses give S_m. With method II and III S_m refers to the variation of the P content only and not to that of the biomass.

In addition to internal translocation, loss via seed released from the panicles and leaching from senescent shoots by rain might explain the decrease of shoot P seen from August onward. On the basis of a seed production amounting to 200 kg. ha^{-1} . y^{-1} (Section 3.1) and a seed P content of 0.424%, loss due to seed shed would amount to 0.8 kg. ha^{-1} . $y^{-1}P$. By December 1975, however, not more than 20% of the seed had left the panicles. In The Netherlands, roughly 50% of the seed leaves the panicles before the 1st of February (Van der Toorn, 1972). Between 10 and 15% of the N that disappears from the shoots in the second half of the growing season is leached by rain (Section 3.1). In general, nutrients are leached from foliage in the order K>N>P (Chapin, 1980). If leaching is taken to amount to 15% of the P decrease in the shoots and loss by seed to 0.4 kg. ha^{-1} . P, we find that 8 kg. ha^{-1} . y^{-1} P. Thus in terms of internal recirculation it may be concluded that about 40% of the 20 kg. ha^{-1} . y^{-1} P required for shoot growth originated from the previous year's shoot after storage in the rhizomes.

P retrieval before leaf abscision in *Molinia* tussocks was estimated to be 83%, corresponding to 1.4 kg. ha⁻¹.y⁻¹ P on the basis of a leaf production amounting to 2 t.ha⁻¹.y⁻¹ (Morton, 1977). Because this concerned a nutrient-poor site, internal circulation must have been the main P supply pathway for the leaf production in the tussocks. The level of internal P recirculation in the reed was not negligible, since it accounted for 8 kg. ha⁻¹.y⁻¹ P or 40% of the above-ground P requirement. The level corresponded roughly with that in reed on the west coast of Sweden (Granéli et al., 1983).

4.2. Phosphorus requirements and availability of phosphorus in the soil

The P requirements of the reed were deduced from the uptake during the 1968-1975 period (Table 4.3). The amount of P in living rhizomes at the end of 1975 (Fig. 4.1) was multiplied by 1.15 to account for dead rhizomes and larger roots (Section 3.1). Fine root material was assumed to be identical with humus accumulating in the 0-100 cm layer from 1968 onward. This accumulation was linear and resulted in an increase of humus amounting to 17 and 11 t.ha⁻¹ in the 0-50 cm and 50-100 cm layer, respectively, during the 1968-1975 period (see also Section 3.6). The P content of the accumulated material was assumed to equal the mean level in the rhizomes sampled in August and December. Shoot production was negligible in 1968, and in 1969 it was about one-third of that in the six years starting in 1970, during which production remained roughly unchanged (Mook & Van

der Toorn, 1982 and pers. comm.). Thus, the duration of the 1968-1975 period was taken at $6\frac{1}{3}$ y. The increase of shoot P during the first half of the growing season and the decrease of it during the second half were taken as 20 and 8 kg. ha⁻¹.y⁻¹ P, respectively. Burning removed 65% of the December shoot biomass (Section 3.2). Thus about 6 of the 9 kg. ha⁻¹ P present in the December shoots ended up in ash and smoke, whereas about 3 kg. ha⁻¹ P persisted in unburned shoot material. If 50% of the P in the burned material left the study area via smoke particles (Lloyd, 1971), 3 kg. ha⁻¹ ash P remained in the litter layer. If we assume complete availability of ash P and assuming 1 kg. ha⁻¹.y⁻¹ P mineralization in the unburned material on the basis of similarity between the rates of P and N mineralization (Section 3.4), the estimated retrieval of P from the litter layer used in Table 4.3 is 4 kg. ha⁻¹.y⁻¹ P.

Table 4.3. Estimated uptake of P (in kg. ha⁻¹) during the 1968-1975 period

Living rhizomes)	
Dead rhizomes)	56 (49 x 1.15)
Roots (> 1 mm ø))	
Fine root material	50 (28000x0.00178)
Shoots	51 (20-8-4)x6.33)
Total uptake	157
Mean uptake per year	25 (157/6.33)

The soils of parcels Nz 23 and Nz 17 were roughly comparable (Ente, 1963). It was assumed that the uptake of P by the reed of parcel Nz 17 (Table 4.3) was roughly equal to that in parcel Nz 23. When the duration of the 1968-1969 period is set at $\frac{1}{3}$ y, as done in Table 4.3, the decrease of citric acid-soluble phosphate (P_{citr}) in the 0-50 cm layer of parcel Nz 23 (Table 4.4) can be described by the following linear regression equation, in which b is the standing stock of P_{citr} in kg. ha⁻¹ P and t is the time in years:

b = 636 - 17.4 t (r = -0.91; P < 0.5%)

Table 4.4. Course of citric acid-soluble phosphate in the soil of parcel Nz 23 from 1968 onward

Sampling date	0-50 cm layer ¹			50-100 cm layer ¹⁾		
	F	P-citr		Available P P		Available P
	(a)	(b)	(c) ²⁾	(a)	(b)	(c) ²
	(mg P ₂ O ₅ /100 g)	(kg ha ⁻¹ P)	(kg ha ⁻¹ P)	(mg P ₂ O ₅ /100 g)	(kg ha ⁻¹ P)	(kg ha ⁻¹ P)
27-8-1968	36.2	658	113	53.7	773	341
23-4-1970	33.1	609	57	54.5	786	353
25-4-1971	34.3	617	77	52.1	752	319
08-5-1972	32.2	577	39	55.1	806	367
21-5-1974	32.5	591	45	52.0	752	318
18-6-1975	29.3	531	-13	56.5	813	381
14-6-1976	28.5	523	-28	53.3	763	334

1) Depths refer to 1975. Due to subsidence, the depth and thickness of corresponding layers decreased from 1968 onward.

Thus, in this layer there was a significant decrease, amounting to 17.4 kg. ha⁻¹.y⁻¹ P_{citr}. In the 50-100 cm layer, Pcitr did not decrease significantly. Total P (not shown) fluctuated irregularly between 2400 and 2700 kg. ha⁻¹ in the 0-50 and between 2200 and 2500 kg. ha⁻¹ in the 50-100 cm layer. Generally leaching of P from clay soils is negligible in The Netherlands (Henkens, 1976). The drainage of plots on clay soil in Oostelijk Flevoland fertilized with 25 and 50 kg. ha-1 P had the same P content as the drainage of unfertilized plots (Habekotté, unpublished). Insignificance of phosphate transport by moving ground-water in these clay soils was also indicated by the nearly complete recovery of fertilizer P in the crop and the top-soil, and by the nearly absence of water-soluble phosphate in the soil of unfertilized plots giving normal crop-yields. If uptake by the reed was solely responsible for the decrease of P_{citr} in the soil, the greater part of the P requirement of 25 kg. ha⁻¹.y⁻¹ P (Table 4.3) must have been withdrawn from the 0-50 cm layer, where the level decreased by 17.4 kg. ha⁻¹.y⁻¹ P_{citr}. In a crop-rotation experiment with cereals and rape-seed on clay soil in Oostelijk Flevoland, yield did not decrease until the P_{citr} content of the 0-64 cm layer had dropped to about 30 mg P₂O₂ per 100 g (Habekotté, 1981; Habekotté & De Jong, 1984). Removal via the crops amounted on average to 23 kg. ha⁻¹.y⁻¹ P. If this critical content of P_{citr} also holds for reed, it is clear from the data in Table 4.4 that the 0-50 cm layer would not have been able to meet the whole P requirement from 1975 onward. In 1975, the original stock of mineral N had decreased considerably down to a depth of 2 m, and roots were present at a depth of at least 2 m (Sections 3.6 and 3.3, respectively). Thus, it seems likely that any required amount of P could be taken up from soil layers down to a depth of 2 m when the 0-50 cm became depleted. By June 1976, the stock of available P in the 50-100 cm layer (Table 4.4) was sufficient to meet the P requirement for more than 10 years.

From P_{oitr} values for parcel Nz 17 in 1972 (not shown) which were about 15% higher than the corresponding values for parcel Nz 23 with respect to the top 1 m layer of the soil, it was concluded that the stock of available P between the depths of 1 and 2 m could meet the requirements of the reed for about 20 years starting in 1976. Considering the negligible leaching and water-solubility of phosphate in these soils, translocation of available P by moving ground-water is unlikely.

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5. General discussion and conclusions

Internal recirculation of N and P was established from the distribution of N and P among shoots and rhizomes during the growing season. A simultaneous increase and decrease in the shoots and rhizomes, respectively, occurred during the first half of the growing season and the reverse during the second half. It was assumed that a decrease in one compartment at any given time was coupled with an increase in the other compartment. Non-simultaneous decreases and increases would mean unlikely N and P spilling in the reed. Nevertheless, Granéli et al. (1983) observed an unexplained 15% decrease of rhizome P during a period of a few weeks before the onset of shoot growth of the reed. Direct proof of internal nutrient translocation ought to be obtainable by the use of isotopes, In a broad sense internal recirculation was demonstrated in reed by Mook & Van der Toorn (1982, 1985), who found a positive correlation between the diameter of the shoots in the spring and the rhizome biomass of the preceding winter, as well as between the latter and the shoot biomass for August and September of the preceding year. Explaining the course of N and P in shoots and rhizomes during the growing season by internal recirculation, it was concluded that between 25 and 50% of the 200 kg N and about 40% of the 20 kg. ha⁻¹.y⁻¹ P required for shoot growth originated from the previous year's shoots after storage in the rhizomes. So, the retrieval percentages for N and P were roughly similar.

With 90 kg. $ha^{-1}.y^{-1}$ N about 65% of the N left in the previous year's shoots was removed by burning. The corresponding figures for P were fixed at 3 kg. $ha^{-1}.y^{-1}$ P and about 35%, respectively. Due to both the considerable removal of shoot N by burning and the rather low mineralization rate of the partly burned shoot remainders, N retrieval from the litter layer was insignificant with 20 kg. ha^{-1} . y^{-1} N, as it meets only 10% of the above-ground requirement at the midst of the growing season. The corresponding figures for P were 4 kg. $ha^{-1}.y^{-1}$ P and 20%, respectively. Thus P retrieval from the litter layer was more important than that of N.

The stock of 1N K_2SO_4 extractable ammonium in the mineral soil was the main N source. In 1975 the upper 2 m of the soil contained enough of this N to meet the requirements of at least three years. The concentration of fixed ammonium in three successive layers down to a depth of 2 m in 1975, in combination with the mineralogical properties of these layers, indicated that the large stores of fixed ammonium had not decreased since emergence in 1968 and thus did not represent a significant N source until the end of 1975. N mineralization, expected in the partially aerated 0-100 cm layer of the close-cropped plots in 1975, was of minor importance. It was estimated at about 50 kg. ha⁻¹.y⁻¹ N.

Between emergence in 1968 and the end of 1975 a standing stock of shoot material, rhizomes, and larger roots, corresponding to about 1200 kg. ha⁻¹ N, was produced, including the amounts lost by burning. Apart from the uptake by the reed, denitrification and immobilization might have reduced the original stores of available N. Tentative figures for denitrification and immobilization were obtained from budgets based on the following assumptions.

- Similarity of the three sites to which the mineral and total soil N figures refer.
- Decrease of mineral N not corresponding with decrease of total N is due to immobilization.
- N supply can only be explained by mineralization, if it cannot be explained by mineral N decrease.
- Uptake of mineral N from upper layers predominates over uptake from deeper layers.
- Mineralization and immobilization in the permanently water-saturated deeper soil layers is no longer significant during the 1968-1975 period.
- Disappearance of mineral N from the soil layers, corresponding with those between a depth of 200 cm and the pleistocene sand in 1975, can be estimated by extrapolation from the disappearance for the layers between 0 and 200 cm.

The N requirements for the production of shoots, rhizomes, and larger roots could be explained by decrease of mineral N and thus were met without mineralization. If the N immobilization according to the budgets reflects storage of mineral N by accumulation of humus, taking the latter as fine root material, the immobilization was larger than corresponded with the humus accumulation in the 1968-1972 period and smaller than that in the 1972-1975 period. The required extra supply at a rate of about 50 kg. ha⁻¹.y⁻¹ N during the latter period was explained by mineralization. The rate was similar to that estimated from the close-cropped fields in 1975.

Any disappearance of mineral N, not ascribed to uptake by the reed vegetation and to immobilization in humus, was ascribed to denitrification. The losses by denitrification - including those by carry off of seeds and draining - amounted to about 100 kg. ha⁻¹ N over the 1968-1975 period. They occurred during the first four years of that period and were within the range of those for undrained reed stands of the polder Oostelijk Flevoland during the first three years after emergence (Van Schreven, 1963^c).

The rather small losses by denitrification contrasted with the high numbers of NH_4^+ -oxidizers in the soil and the limited capacity of the reed to absorb nitrate. The numbers of NH_4^+ -oxidizers as well as the nitrate-reductase activity and the nitrate content of the shoots were lower when the water level was higher. It indicates that in the permanently water-saturated soil layers below a depth of 1 m, where the stores of $1N K_2SO_4$ extractable NH_4^+ -N in 1978 were far from exhausted (unpubl.), nitrification was limited because the oxygen supply by leakage from the roots was insufficient. Insignificant denitrification losses associated with a marsh species having oxygen-releasing roots were also reported by Buresh et al. (1981). The rather efficient N economy found for the dry reeds stands in the polder Zuidelijk Flevoland was based both on internal recycling and efficient utilization of mineral N. In the deeper soil layers with an oxygen-limited nitrification and a root-directed mass flow, uptake of any nitrate by the roots apparently predominated over uptake by denitrifiers. In the aerated upper soil layers low denitrification losses were probably due to rapid exhaustion of the NH_4^+ -N stock by the reed.

The stock of citric acid-soluble phosphate (P_{citr}) in the 0-50 cm layer was the main P source during the 1968-1975 period. When no burning or equivalent management measure was applied to prevent infestation by insects, the production decreased in the dry stands starting in 1972, which was three years after the reed had been sown (Van der Toorn & Mook, 1982; Mook & Van der Toorn, 1982). In the burned stands a decrease in production due to N shortage was not expected within 10 years starting in 1968. In view of the stock of citric acid-soluble P in the soil layers down to a depth of 2 m, P shortage would not be expected within four decades starting in 1968.

6. References

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Date of sampling	Above-groui	nd samples	Below-ground samples		
	Area per sample (m²)	Number of samples	Area per sample (cm ²)	Number of samples	
14 March 1974	0.25	8			
12 April 1974	0.25	8			
3 August 1974	0.25	5	2,500 ²⁾	5	
-	1.00 ¹⁾	3			
27 November 1974	0.25	7	2,500 ²⁾	5	
	1.00 ¹⁾	3			
4 March 1975	0.25	10			
24 March 1975			1,252	5	
24 April 1975	0.25	10			
4 June 1975	0.50	5	1,252	5	
13 August 1975	0.25	20	407	20	
30 September 1975	0.25	5	203	5	
7 November 1975	0.25	3			
	1.001)	2			
7 December 1975	0.25	15	407	20	
	1.00 ¹⁾	5			

Appendix 1. Area and number of reed samples; see also Section 2.2.

 Quadrats in which the reed grew up through netting placed on the soil surface after burning.
 Area of the quadrats on which the soil was dug out to collect the rhizomes. All other areas for below-ground sampling are based on combinations of 3 to 6 soil cores.

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Appendix 2. Calculation of litter N expected after burning of 1975; amounts are in kg. ha⁻¹ (see also Section 3.4.2)

Litter layer in 1972 before burning	327	([140/3] + 140 + 140)
Litter layer in 1972 after burning	117	(327 x 50/140)
Litter layer in 1975 after burning	267	(117 + 50 + 50 + 50)

Appendix 3. Calculation of mineral N disappeared from the soil below layer II during the 1968-1972 period; corresponding layers are indicated by A or B; amounts are in kg. ha⁻¹ mineral N (see also Section 3.6.1)

Stock of 123-150 cm layer (A) in 1968	252	
Stock of 107-134 cm layer (A) in 1972	153	
Disappeared from layer A	99	(252-153)
Stock of 167-218 cm layer (B) in 1968	504	
Stock of 150-200 cm layer (B) in 1972	470	
Disappeared from layer B	34	(504-470)
Disappeared from the soil between A and B	48	(interpolation)
Disappeared from below B	≈0	(extrapolation)
Total disappeared from below layer II	181	(99+34+48+0)

Appendix 4. Calculation of mineral N disappeared from the soil between layer II and the 200 cm level; corresponding layers are indicated by C; amounts are in kg. ha⁻¹ mineral N (see also Section 3.6.2)

Stock of 0-210 cm layer (C) in 1972	1015	
Stock of 0-200 cm layer (C) in 1975	603	
Disappeared from layer C	412	(1015-603)
Disappeared from layers I and II	125	(table 3.9) ¹⁾
Disappeared from the soil between		
layer II and 200 cm (depth in 1975)	287	(412-125)

1) 31 - 12 + 118 - 12 = 125

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