Wetlands Ecol Manage (2014) 22:157–176
DOI 10.1007/s11273-014-9336-8

ORIGINAL PAPER

A simulation model for nitrogen cycling in natural rooted papyrus wetlands in East Africa

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Received: 31 May 2013 / Accepted: 2 January 2014 / Published online: 23 January 2014

Abstract Papyrus (*Cyperus papyrus*) wetlands around East African lakes provide important ecosystem services, including retention of nutrients, to millions of people. To understand the processes contributing to nitrogen retention in the wetland and to evaluate the effects of papyrus harvesting, a dynamic model for carbon and nitrogen cycling in rooted papyrus wetlands was constructed. The model consisted of sub-models for the permanently (P) and seasonally (S) flooded zones and was based on data from a papyrus wetland in Naivasha, Kenya. In each zone, water, nitrogen and carbon flows were calculated based on descriptions of hydrological (river flow, lake level, precipitation, evaporation) and ecological (e.g. photosynthesis, nitrogen uptake, mineralisation, nitrification) processes. Literature data were used for parameterization and calibration. The model simulated realistic concentrations of dissolved nitrogen and papyrus biomass density of papyrus. Daily harvesting up to about 84 (S-zone) and 60 (P-zone) g/m^2 days dry weight reduced the aboveground biomass and increased nitrogen retention (expressed as $(N_{inflow} - N_{outflow})/N_{inflow} * 100\%$) to 38 % (S-zone) and 50 % (P-zone). A further increase in daily harvesting resulted in collapse of the aboveground biomass. Papyrus biomass, however, recovered fully from annual harvesting of up to 100 % of the biomass. The model showed that papyrus re-growth after harvesting is nitrogen-limited in the P-zone.

Keywords Nitrogen · Lake Naivasha · Wetlands · Modelling · Nitrogen retention · Regulating ecosystem services

Electronic supplementary material The online version of this article (doi:10.1007/s11273-014-9336-8) contains supplementary material, which is available to authorized users.

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Introduction

Wetlands dominated by *Cyperus papyrus* are important ecosystems in East and Central Africa because they provide important ecosystem functions and services for millions of people, including provisioning services for building, crafts and fuel, water, food and medicinal herbs (Geheb and Binns 1997; Kipkemboi et al. 2007; Mwakubo and Obare 2009; Kabumbuli and Kiwazi 2009), and regulating ecosystem services such as sediment and nutrient retention or flood regulation (Mwanuzi et al. 2003; Loiselle et al. 2008).

They provide a habitat for mammals, birds and fish (Gichuki and Gichuki 1992; Maclean et al. 2006; van Dam et al. 2011). Papyrus vegetation can be rooted in the sediment, or through the action of wind and waves, become detached to form floating mats (Azza et al. 2006). Papyrus wetlands thus often show zones with distinct hydrological character: a floating outer fringe; a permanently flooded zone, in which the soil is saturated year-round and *C. papyrus* is the dominant species; and a seasonally flooded zone, which can be dry during part of the year (Denny 1984).

In decision making about wetlands, provisioning services often get priority over regulating services despite the fact that regulating services generally have the higher monetary value (Stuip et al. 2002; Emerton 2005). Regulating services are difficult to value and appreciate because of a lack of knowledge of the underlying processes. Lacking clear commodity prices; their value must be estimated using indirect methods (De Groot et al. 2006). Many papyrus wetlands are under pressure, driven by population growth and economic development. Structural changes to the wetland like conversion to cropland, construction of irrigation and drainage canals, fish traps and hippo ditches affect the ecological functioning of the system. Livelihoods activities enhance the provisioning services of the wetlands but reduce the regulating services, thus disturbing the balance among ecosystem services important for sustainable management (TEEB 2010; Maltby and Acreman 2011). Better quantitative understanding of regulating services of wetlands, and of their dynamics under the influence of natural and anthropogenic pressures is required (Carpenter et al. 2009).

Nutrient retention in wetlands depends on hydrology, atmospheric flux of nitrogen, phosphorus adsorption capacity of the soil, and export of nutrients through vegetation harvesting. Uptake of nutrients is related directly to the growth rate of the plants, with papyrus capable of absorbing large quantities of nutrients from soil to water during the exponential growth phase. Nutrient uptake is reduced when growth rate decreases because of suboptimal soil wetness or maturity of the vegetation (van Dam et al. 2007). Nutrients contained in vegetation are released during senescence. Harvesting of plants affects nutrient balances, in two ways. First, nutrients are simply removed. Second, reduced biomass of the vegetation stimulates re-growth and nutrient uptake. Denitrification and biological nitrogen fixation influence the nitrogen balance of the wetland directly, but little is known about these processes in papyrus wetlands (van Dam et al. 2011).

Retaining nutrients in wetlands reduces enrichment of downstream water bodies. Eutrophication in the East African lakes has a direct impact on the local economies as water ways get blocked by excessive growth of water hyacinth and fish catches reduce due to algal blooms. The impact of papyrus on downstream nitrogen concentrations is higher than on phosphorus concentrations as papyrus contains more N (the median N:P ratio of papyrus in ten different sites was 19.85; Gaudet 1975). Therefore a model to simulate nitrogen in a papyrus wetland to compare the effects of wetness and harvesting on outflow concentrations will be useful for determining trade-offs between provisioning services (harvesting) and regulating services (nutrient retention).

The overall aim of this study is to better understand the effects of harvesting and hydrology on nitrogen retention in rooted papyrus wetlands. Specific objectives were: (1) to construct a dynamic simulation model of rooted papyrus growth in both seasonally and permanently flooded zones; (2) to parameterize and calibrate the model with a dataset from Lake Naivasha in Kenya; (3) to assess the effects of hydrological conditions and harvesting on nitrogen retention.

Methods

System description and model development

Lake Naivasha papyrus wetland is one of the best studied papyrus systems (e.g. Gaudet 1979; Jones and Muthuri 1997; Becht et al. 2006; Boar 2006). Owing to water level fluctuations and cultivation, the area covered by *C. papyrus* declined from around 50 to 5–10 km^2 between 1960 and 2000 (Hickley et al. 2004). Studies between 1993 and 2001 showed that mean dry weight (DW) biomass was 6.9 g/m^2, with approximate culm densities of 30 culms/m^2 and plant height of up to 4 m (Boar 2006). The north swamp in Naivasha is located at the mouth of the Malewa River which floods the wetland for short periods during the rainy season (Boar and Harper 2002). At the lakeward side, the wetland is flooded by lake water.

Based on this situation, a conceptual model for a rooted papyrus wetland was constructed (Fig. 1).

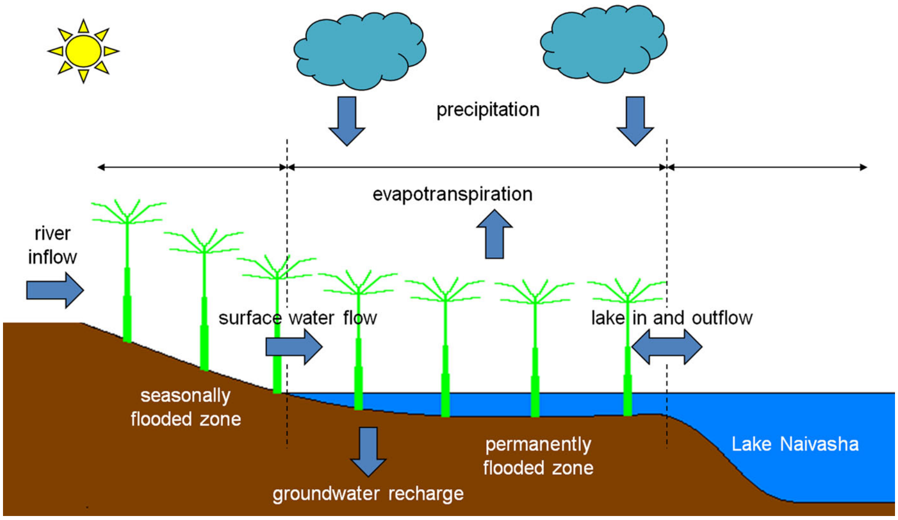

Fig. 1 Conceptual model of the papyrus wetlands bordering Lake Naivasha

River water floods the seasonal (S) zone and then the permanent (P) zone. Depending on the water level of the lake, the P-zone discharges into or receives backflow from the lake. Because of the slope of the S-zone, the surface water flows towards the P-zone and there is no standing water in the S-zone. Precipitation, evapotranspiration and groundwater flows affect the water depth in the wetland. The model assumes a monospecific stand of *C. papyrus*.

Several models of the role of vegetation in the nutrient cycling of wetlands have been developed. Van der Peijl and Verhoeven (1999) modelled a sloping wetland at Kismeldon Meadows, Devon, SouthWestern England. The model describes the carbon, nitrogen and phosphorus dynamics, their interactions in a riverine wetland with a vegetation dominated by *Molinia caerulea* and how these are affected by soil wetness and temperature. Based on descriptions of basic processes such as photosynthesis, nutrient uptake and decomposition the model describes the nutrient cycles and plant growth reasonably well. Van Dam et al. (2007) constructed a model of a floating papyrus wetland in Jinja, Uganda. This model described the flows of nitrogen through the papyrus vegetation and various compartments of detritus, and predicted the effects of vegetation harvesting on the water quality under the floating mat. These two models were used as the basis for the new papyrus model. A new model was needed as the existing models focus on different plant species and climate (Kismeldon Meadows) or on floating papyrus (Jinja) and therefore do not sufficiently cover the processes and components of a rooted papyrus wetland.

Equations, variables and constants

Table 1 lists the state variables used and Table 2 presents all processes with equations. Key variables and processes are presented below in the model description, in which numbers behind variables or processes refer to the state variables in Table 1 or to equations in Table 2. A complete list of variables and constants is provided in Online Resource 1. The model was built using STELLA 9.1.4 (High Performance Systems, Hanover, NH) and run for a period of 5 years with rectangular (Euler) integration and a time step of 0.0625 days (1.5 h) for 1 m^2 of wetland. A complete listing of the equation layer of the Stella model can be found in Online Resource 2.

Model assumptions and implementation

The model assumes an even distribution of water in the wetland without channels or preferential flow. Because of the slope in the S-zone, surface water flows towards the P-zone and there are no pools in the S-zone. All papyrus plants are rooted, and floating papyrus mats at the edge of the lake are not considered. Phosphorus, sulphur and other elements needed for growth are assumed not to be limiting and not included in the model. Growth is limited when there is no water to provide ammonium or nitrate. The model does not

Table 1 State variables

Variable	Description	#	Initial value	Unit	Source
WaterS	Water level seasonally flooded wetland	1	0.2	m^3/m^2	a
WaterP	Water level permanently flooded wetland	2	0.5	m^3/m^2	a
CAGBS	C aboveground biomass seasonally flooded	3	1,853	g C/m^2	b
CBGBS	C belowground biomass seasonally flooded	4	1,570	g C/m^2	b
CDAGBS	C dead AGB seasonally flooded	5	335	g C/m^2	c
CDBGBS	C dead BGB seasonally flooded	6	284	g C/m^2	c
POCS	Particulate organic carbon seasonally flooded	7	20	g C/m^2	a
CAGBP	C aboveground biomass permanently flooded	8	1,853	g C/m^2	b
CBGBP	C belowground biomass permanently flooded	9	1,570	g C/m^2	b
CDAGBP	C dead AGB permanently flooded	10	335	g C/m^2	c
CDBGBP	C dead BGB permanently flooded	11	284	g C/m^2	c
POCSP	POC surface water permanently flooded	12	20	g C/m^2	a
POCPP	POC pore water permanently flooded	13	20	g C/m^2	a
NAGBS	N aboveground biomass seasonally flooded	14	44	g N/m^2	d
NBGBS	N belowground biomass seasonally flooded	15	31	g N/m^2	d
NDAGBS	N dead AGB seasonally flooded	16	7.9	g N/m^2	c
NDBGBS	N dead BGB seasonally flooded	17	5.6	g N/m^2	c
PONS	Particulate organic nitrogen seasonally flooded	18	0.9	g N/m^2	e
DONS	Dissolved organic nitrogen seasonally flooded	19	1.1	g N/m^2	e
NO3S	Nitrate seasonally flooded	20	0.05	g N/m^2	e
NH4S	Ammonium seasonally flooded	21	0.5	g N/m^2	e
NH4AS	Ammonium adsorbed seasonally flooded	22	5	g N/m^2	a
NAGBP	N aboveground biomass permanently flooded	23	44	g N/m^2	d
NBGBP	N belowground biomass permanently flooded	24	31	g N/m^2	d
NDAGBP	N dead AGB permanently flooded	25	7.9	g N/m^2	c
NDBGBP	N dead BGB permanently flooded	26	5.6	g N/m^2	c
PONSP	PON surface water permanently flooded	27	0.9	g N/m^2	e
PONPP	PON pore water permanently flooded	28	0.9	g N/m^2	e
DONSP	DON surface water permanently flooded	29	1.1	g N/m^2	e
DONPP	DON pore water permanently flooded	30	1.1	g N/m^2	e
NH4SP	Ammonium surface water permanently flooded	31	0.5	g N/m^2	e
NH4PP	Ammonium pore water permanently flooded	32	0.5	g N/m^2	e
NO3SP	Nitrate surface water permanently flooded	33	0.05	g N/m^2	e
NO3PP	Nitrate pore water permanently flooded	34	0.05	g N/m^2	e
NH4AP	Ammonium adsorbed permanently flooded	35	0.5	g N/m^2	a

a estimate, *b* average of Boar et al. (1999) Jones and Humphries (2002) Boar (2006), *c* calculated, see Online Resource 1, *d* average of Boar et al. (1999) Boar (2006), *e* Muthuri and Jones (1997)

include nitrogen fixation, nitrogen deposition and ammonia volatilization. Nitrogen fixation in papyrus wetlands is poorly quantified (Mwaura and Widdowson 1992; Gichuki et al. 2005). Ammonia volatilization is not expected to play a big role as the pH in papyrus wetlands is low (Azza et al. 2000). Nitrogen (wet and dry) deposition in East Africa is estimated at 0.5 g N/m^2 year (Dentener et al. 2006), which is less than 0.5 % of the total N inflow used in the model simulations.

Table 2 Rate variables (processes) in the model

Process	Description	Equation	#
Lake_Inflow	Lake inflow	IF(surfw_P < threshold__swd_P) THEN(lake_inflow_rate) ELSE(0)	36
Outflow	Outflow of P wetland	IF(surfw_P > threshold__swd_P) THEN(surface_water_flow + prec_P-evap_P-recharge_P) ELSE(0)	37
Prec_P	Precipitation	Rainfall_rate*0.001	38
Evap_P	Evaporation	Evaporation_rate*0.001	39
Recharge_P	Groundwater recharge	Frout_P*porew_free_P	40
Surface_water_flow	Surface water flow from S to P wetland	Froff_S*surfw_S	41
Evap_S	Evaporation	Evaporation_rate*0.001	42
Prec_S	Precipitation	Rainfall_rate*0.001	43
Inflow_S	Inflow S wetland	River_inflow_rate/area_S	44
Recharge_S	Groundwater recharge	Frout_S*porew_free_S	45
CAGBS_harvest_D	Daily harvesting AGB	(PULSE (harvest_in_g_C, harvest_day-1, harvest_interval))*harvest_in_S_yes_or_no	46
CAGBS_harvest_A	Annual harvesting AGB	(PULSE (CAGBS*harvest_ %, harvest_day-1, harvest_interval))*harvest_in_S_yes_or_no	47
CAGBS_respiration	Respiration AGB	CAGBS*maintenance_coefficient + CAGBS_assimilation*growth_coefficient	48
CAGBS_assimilation	CO_2 uptake AGB	Max_assimilation_constant*CAGBS*limit_radiance*(limit_N_S/0.9)* ((max_AGB_biomass*perc_C_in_AGB-CAGBS)/max_AGB_biomass*perc_C_in_AGB)	49
CAGBS_death	Death of AGB	CAGBS*CAGB_death_constant	50
CDAGBS_leach	Leaching from DAGB	CDAGB_leach_constant*CAGBS_death	51
CDAGBS_frag	Fragmentation of DAGB	CDAGBS*CDAGB_frag_constant	52
POCS_hydrolysis	Hydrolysis of POC	POCS*POC_hydrolysis_constant	53
CDBGBS_frag	Fragmentation of DBGB	CDBGBS*CDBGB_frag_constant	54
CDBGBS_leach	Leaching from DBGB	CDBGB_leach_constant*CBGBS_death	55
CBGBS_death	Death of BGB	CBGBS*CBGB_death_constant	56
CBGBS_respiration	Respiration BGB	CBGBS*maintenance_coefficient + C_trans_S*growth__coefficient	57
			58
C_trans_S	Translocation	(CAGBS-CBGBS*C_AGB_to_BGB_optimal_ratio)/(1 + C_AGB_to_BGB_optimal_ratio)	59
CAGBP_harvest_D	Daily harvesting AGB	PULSE(harvest_in_g_C, harvest_day-1,harvest_interval)	60
CAGBP_harvest_A	Batch harvesting AGB	PULSE(CAGBP*harvest_ %, harvest_day-1,harvest_interval)	61
CAGBP_respiration	Respiration AGB	CAGBP*maintenance_coefficient + CAGBP_assimilation*growth_coefficient	62
CAGBP_assimilation	CO_2 uptake AGB	Max_assimilation_constant*CAGBP*limit_radiance*limit_NP_P*((max_AGB_biomass*perc_C_in_AGB-CAGBP)/(max_AGB_biomass*perc_C_in_AGB))	63
CAGBP_death	Death of AGB	CAGBP*CAGB_death_constant	64
CDAGBP_leach	Leaching from DAGB	CDAGB_leach_constant*CAGBP_death	65
CDAGBP_frag	Fragmentation of DAGB	CDAGBP*CDAGB_frag_constant	66
POCSP_hydrolysis	Hydrolysis of POC in surface water	POCSP*POC_hydrolysis_constant	67
POCPP_hydrolysis	Hydrolysis of POC in pore water	POCPP*POC_hydrolysis_constant	68
POCSP_settling	Settling of POC	POCSP*POC_settling_rate	69
CDBGBP_frag	Fragmentation of DBGB	CDBGBP*CDBGB__frag_constant	70
CDBGBP_leach	Leaching from DBGB	CDBGB_leach_constant*CBGBP_death	71
CBGBP_death	Death of BGB	CBGBP*CBGB_death_constant	72
CBGBP_respiration	Respiration BGB	CBGBP*maintenance_coefficient + C_trans_P*growth__coefficient	73
C_trans_P	Translocation	(CAGBP−CBGBP*C_AGB_to_BGB_optimal_ratio)/(1 + C_AGB_to_BGB_optimal_ratio)	74
NAGBS_harvest_D	Daily harvesting AGB	CAGBS_harvest_D/CN_AGBS_ratio	75

Table 2 continued

Process	Description	Equation	#
NAGBS_harvest_B	Batch harvesting AGB	IF(CN_AGBS_ratio > 0)THEN(CAGBS_ harvest_B/CN_AGBS_ratio)ELSE(0)	76
NAGBS_death	Death of AGB	CAGBS_death*(1−N_retrans_constant)/CN_AGBS_ratio	77
NDAGBS_frag	Fragmentation of DAGB	CDAGBS_frag/CN_DAGBS_ratio	78
PONS_inflow	Inflow of particulate organic nitrogen	PONS_load	79
PONS_hydrolysis	Hydrolysis of PON	PONS*PON_hydrolysis_constant	80
DONS_inflow	Inflow of dissolved organic nitrogen	DONS_load	81
DONS_outflow	Outflow of DON	Surface_water_flow*conc_DONS	82
DONS_mineral	Mineralisation	DONS*K_mineral	83
DONS_recharge	Groundwater recharge	Conc_DONS*recharge_S	84
PONS_outflow	PON outflow	Surface_water_flow*conc_PONS	85
NDBGBS_frag	Fragmentation	CDBGBS_frag/CN_DBGBS_ratio	86
PONS_recharge	Groundwater recharge	Conc_PONS*recharge_S	87
NH4S_outflow	NH_4 outflow	Surface_water_flow*conc_NH4S	88
NH4S_adsorption	Adsorption	IF(conc_NH4S > 5)THEN(K_NH4_adsorption*NH4S) ELSE(−K_NH4_adsorption*NH4AS))	89
NH4S_recharge	Groundwater recharge	Conc_NH4S*recharge_S	90
NDBGBS_leach	Leaching from DBGB	CDBGBS_leach/CN_DBGBS_ratio	91
NH4S_inflow	NH_4 inflow	NH4S_load	92
NDAGBS_leach	Leaching from DAGB	CDAGBS_leach/CN_DAGBS_ratio	93
NH4S_uptake	Uptake by papyrus	Max_NH4_uptake*N_papyrus_S*(1−N_papyrus_S/ N_max_papyrus)*limit_NH4S	94
Nitri_S	Nitrification	K_nitri*mode_S*NH4S	95
NO3S_outflow	NO_3 outflow	Surface_water_flow*conc_NO3S	96
NO3S_recharge	Groundwater recharge	Conc_NO3S*recharge_S	97
Denitri_S	Denitrification	K_denitri*NO3S*(1−mode_S)	98
NO3S_inflow	NO_3 inflow	NO3S_load	99
NO3S_uptake	Uptake by papyrus	Max_NO3_uptake*N_papyrus_S*(1−N_papyrus_S/ N_max__papyrus)*limit_NO3S	100
NBGBS_death	Death of BGB	CBGBS_death/CN_BGBS_ratio	101
N_trans_S	Translocation	(NAGBS−NBGBS*C_AGB_to__BGB_ratio_S)/ (C_AGB_to_BGB_ratio_S + 1)	102
N_retrans_S	Retranslocation	CAGBS_death*N_retrans_constant/CN_AGBS_ratio	103
NAGBP_harvest_D	Daily harvesting AGB	CAGBP_harvest_D/CN_AGBP_ratio	104
NAGBP_harvest_B	Batch harvesting AGB	IF(CN_AGBP_ratio > 0)THEN(CAGBP_harvest_B/CN_ AGBP_ratio)ELSE(0)	105
NAGBP_death	Death of AGB	CAGBP_death*(1−N_retrans_constant)/CN_AGBP_ratio	106
NDAGBP_leach	Leaching from DABG	CDAGBP_leach/CN_DAGBP_ratio	107
NDAGBP_frag	Fragmentation	CDAGBP_frag/CN_DAGBP_ratio	108
PONSP_lake_in	PON inflow lake	Lake_Inflow*conc_PON__lake_inflow	109
PONSP_settling	Settling of PON	PONSP*PON_settling_constant	110
PONSP_surf_in	PON inflow surface water	Surface_water_flow*conc_PONS	111
PONSP_outflow	PON outflow	Outflow*conc_PONSP	112
PONSP_hydrolysis	Hydrolysis of PON in surface water	PONSP*PON_hydrolysis_constant	113
DON_w_lake_in	DON inflow lake	Lake_Inflow*conc_DON__lake_inflow	114
DON_w_surf_in	DON inflow surface water	Surface_water_flow*conc_DONS	115
DONP_diffusion	DON diffusion between surface and pore water	IF(surfw_P > 0) THEN(K_DON_diffusion* ((DONSP/surfw_P)−(DONPP/soil_depth_P))/ ((surfw_P + soil_depth_P)/2)) ELSE(0)	116
DONSP_outflow	DON outflow	Outflow*conc_DONSP	117
DONSP_mineral	Mineralisation in surface water	K_mineral*DONSP	118
NH4_lake_in	NH_4 inflow lake	Lake_Inflow*conc_NH4_lake_inflow	119

Table 2 continued

Process	Description	Equation	#
NH4S_in	NH_4 inflow surface water	Surface_water_flow*conc_NH4S	120
NH4P_diffusion	NH_4 diffusion between surface and pore water	IF(surfw_P > 0) THEN(K_NH4_diffusion*((NH4SP/surfw_P)−(NH4PP/soil_depth_P))/((surfw_P + soil_depth_P)/2)) ELSE(0)	121
NH4SP_outflow	NH_4 outflow	outflow*conc_NH4SP	122
Nitri_SP	Nitrification surface water	K_nitri*NH4SP	123
NH4P_adsorption	Adsorption	(IF(conc_NH4PP > 5)THEN(NH4PP*K_NH4_adsorption)ELSE(−2*K_NH4_adsorption*NH4AP))	124
NO3S_in	NO_3 inflow surface water	surface_water_flow*conc_NO3S	125
NO3_lake_in	NO_3 inflow lake	lake_Inflow*conc_NO3__lake_inflow	126
NO3SP_outflow	NO_3 outflow	outflow*conc_NO3SP	127
NO3P_diffusion	NO_3 diffusion between surface and pore water	IF(surfw_P > 0) THEN(K_NO3_diffusion*((NO3SP/surfw_P)−(NO3PP/soil_depth_P))/((surfw_P + soil_depth_P)/2)) ELSE(0)	128
Denitri_PP	Denitrification	K_denitri*NO3PP*(1−mode_P)	129
NO3P_recharge	Groundwater recharge	conc_NO3PP*recharge_P	130
NO3_uptake_P	NO_3 uptake by papyrus	max_NO3_uptake*N_papyrus_P*(1−N_papyrus_P/N_max_papyrus)*limit_NO3PP	131
Nitrifi_PP	Nitrification pore water	K_nitri*mode_P*NH4PP	132
NH4P_recharge	Groundwater recharge	conc_NH4PP*recharge_P	133
NDBGBP_leach	Leaching from DBGB	CDBGBP_leach/CN_DBGBP_ratio	134
NH4_uptake_P	NH_4 uptake by papyrus	max_NH4_uptake*N_papyrus_P*(1−N_papyrus_P/N_max_papyrus)*limit_NH4PP	135
DONPP_mineral	Mineralisation	K_mineral*DONPP	136
PONPP_hydrolysis	Hydrolysis of PON in pore water	PONPP*PON_hydrolysis_constant	137
DONP_recharge	Groundwater recharge	conc_DONPP*recharge_P	138
PONP_recharge	Groundwater recharge	conc_PONPP*recharge_P	139
NDBGBP_frag	Fragmentation	CDBGBP_frag/CN_DBGBP_ratio	140
NBGBP_death	Death of BGB	CBGBP_death/CN_BGBP_ratio	141
N_trans_P	Translocation	(NAGBP−NBGBP*C_AGB_to_BGB_ratio_P)/(C_AGB_to_BGB_ratio_P + 1)	142
N_retrans_P	Retranslocation	CAGBP_death*N_retrans_constant/CN_AGBP_ratio	143

Parameterization and calibration

The model was parameterized and calibrated with literature data available for Lake Naivasha (Online Resource 1). When values from Lake Naivasha were not available, data from other East African papyrus wetlands were used. For parameters that were never studied or measured in papyrus wetlands, literature values from other wetland types were used or values estimated (Table 1 and Online Resource 1). Seasonal variability in the Lake Naivasha wetland was described using monthly averages from the period 1970 to 1982 for irradiance (Muthuri et al. 1989), evaporation and precipitation from the period 1974 to 1976 (Gaudet 1979) and river inflow. River inflow had different values for each month, based on the flow regime of the Malewa River (Gaudet 1979) and was calibrated to achieve realistic flow rates and nitrogen concentrations. River flow followed a similar seasonal pattern as rainfall (Fig. 5), with a main rainy season in the months March, April and May and a short rainy season in December. Inflow in the dry season (0.09 m/day) was about half of the inflow at the peak of the rainy season (0.19 m/day). The peak rainfall (0.19 m/day) was equal to the maximum inflow rate. During most of the year rainfall was lower than inflow. Evaporation varied throughout the year between 0.10 and 0.15 m/day. There was an outflow of the P-zone during about 130 days per year with a peak of 0.33 m/day. The rest of the year there was a backflow from the lake of between 0 and 0.12 m/day. This hydrological regime was repeated annually.

Hydrology sub-model

The hydrology sub-model (Fig. 2) calculates the water level in S and P-zones (as the volume of water per m^2

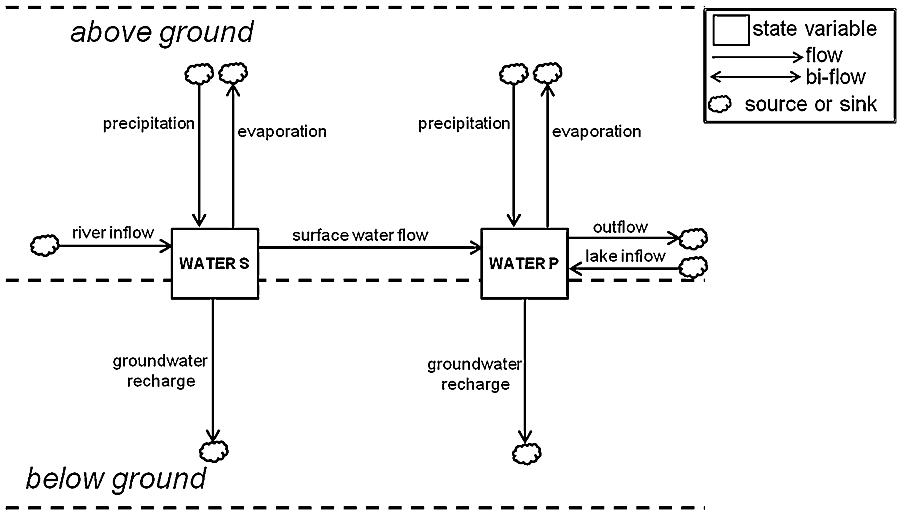

Fig. 2 Conceptual diagram of the hydrology sub-model (WATER S = water level in the seasonal zone; WATER P = water level in permanent zone)

of surface area) based on river discharge into the S-zone, surface water flow from the S-zone into the P-zone, outflow and backflow between the P-zone and the lake, and precipitation, evaporation and groundwater recharge in both S-zone and P-zone. River discharge, precipitation and evaporation were based on observed data (Gaudet 1979). Groundwater recharge was modelled with first order equations (Eqs. 40 and 45). If the soil is saturated, 1 % of the pore space above the water filled porosity is recharged, resulting in a maximum recharge of 0.6 mm per day.

The term MODE (Online Resource 1) controls the availability of oxygen in the wetland. This is important as oxygen availability controls nitrification and denitrification rates. Based on the amount of water and on soil volume and porosity, the water filled porosity is calculated and compared with the water filled porosity at field capacity. Below field capacity, conditions are aerobic (MODE = 1). When the soil is fully saturated or flooded, conditions are anaerobic (MODE = 0). Between field capacity and saturation, the value of MODE is related linearly to the proportion of pore space filled (MODE between 0 and 1).

Carbon sub-models

Papyrus biomass was modelled as carbon in aboveground (culms and umbels) and belowground (rhizome and roots) biomass (Fig. 3). Carbon in the aboveground biomass (CAGB) results from assimilation (photosynthesis) and translocation of carbon from the rhizome. Assimilation (Eqs. 49, 63) was modelled as a logistic model depending on aboveground biomass, and limited by irradiance and the availability of nitrate and ammonium (both Monod-type equations):

$$\begin{aligned}\text{Assimilation} &= \text{max\_assimilation\_constant} \times \text{CAGB} \\ &\times \frac{\text{radiance}}{(\text{radiance} + \text{K\_radiance})} \times \frac{\text{limit\_N}}{0.9} \\ &\times \frac{(\text{max\_AGB\_biomass} \cdot \text{perc\_C\_in\_AGB} - \text{CAGB})}{\text{max\_AGB\_biomass} \cdot \text{perc\_C\_in\_AGB}}\end{aligned}$$

in which max_assimilation_constant is the maximum relative assimilation rate (day^{-1}), CAGB is carbon in the aboveground biomass (g C/m^2), radiance is irradiance (MJ/m^2 day), K_radiance is the half saturation constant of irradiance for assimilation (MJ/m^2 day), limit_N is limiting factor of N for carbon assimilation (dimensionless; see Online Resource 1), the factor 0.9 ensures that maximum growth limitation can be reached (van der Peijl and Verhoeven 1999), max_AGB_biomass is the maximum AGB biomass (g/m^2), and perc_C_in AGB is the carbon content (dry weight) of aboveground biomass (%).

It was assumed that whenever the nitrogen concentration in papyrus was below the minimum needed

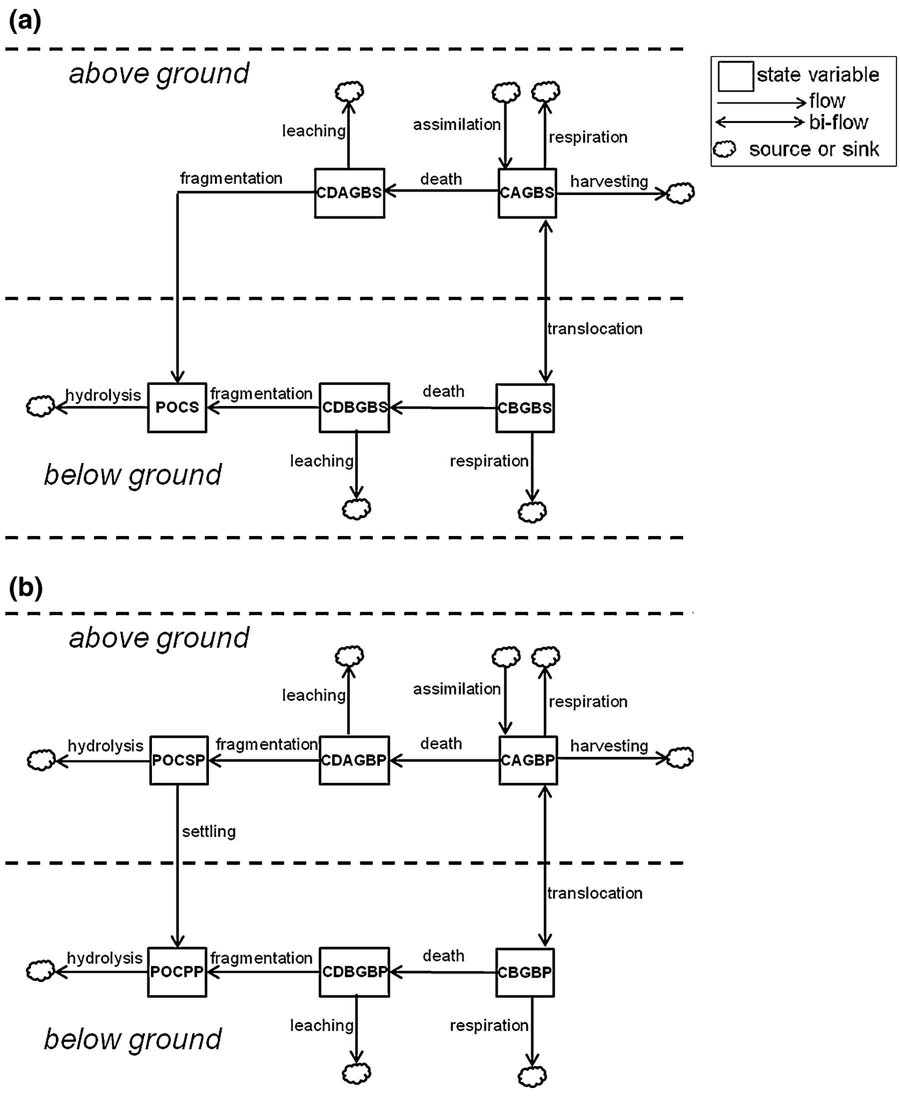

Fig. 3 Conceptual diagram of the carbon sub-model for the seasonally flooded zone (**a**) and permanently flooded zone (**b**) (names of state variables are explained in Table 1)

for assimilation (0.0016 g N/g DW; van der Peijl and Verhoeven 1999), there was no growth (limit_N_P and limit N_S, Online Resource 1) so a Monod-type function with a cut-off was used.

Translocation of carbon between aboveground and belowground biomass (Eqs. 59, 74) was based on an assumed optimal ratio between aboveground and belowground carbon (C_AGB_to_BGB_optimal_ratio, Online Resource 1), of 1.2 (Boar et al. 1999; Jones and Humphries 2002). Whenever carbon ratio differed from this optimal ratio, carbon was translocated to restore the optimum:

$$\text{Translocation} = \frac{(\text{CAGB} - \text{CBGB} \times \text{optimal\_C\_AGB/C\_BGB})}{(1 + \text{optimal\_C\_AGB/C\_BGB})}$$

in which CAGB and CBGB are carbon in aboveground and belowground biomass, respectively (g C/m^2), and optimal_C_AGB/C_BGB is the optimal ratio between carbon in aboveground and belowground biomass (g C/m^2).

Other processes leading to a reduction in CAGB were respiration (the sum of maintenance and growth respiration; Eqs. 48 and 57) and harvesting (Eqs. 46,

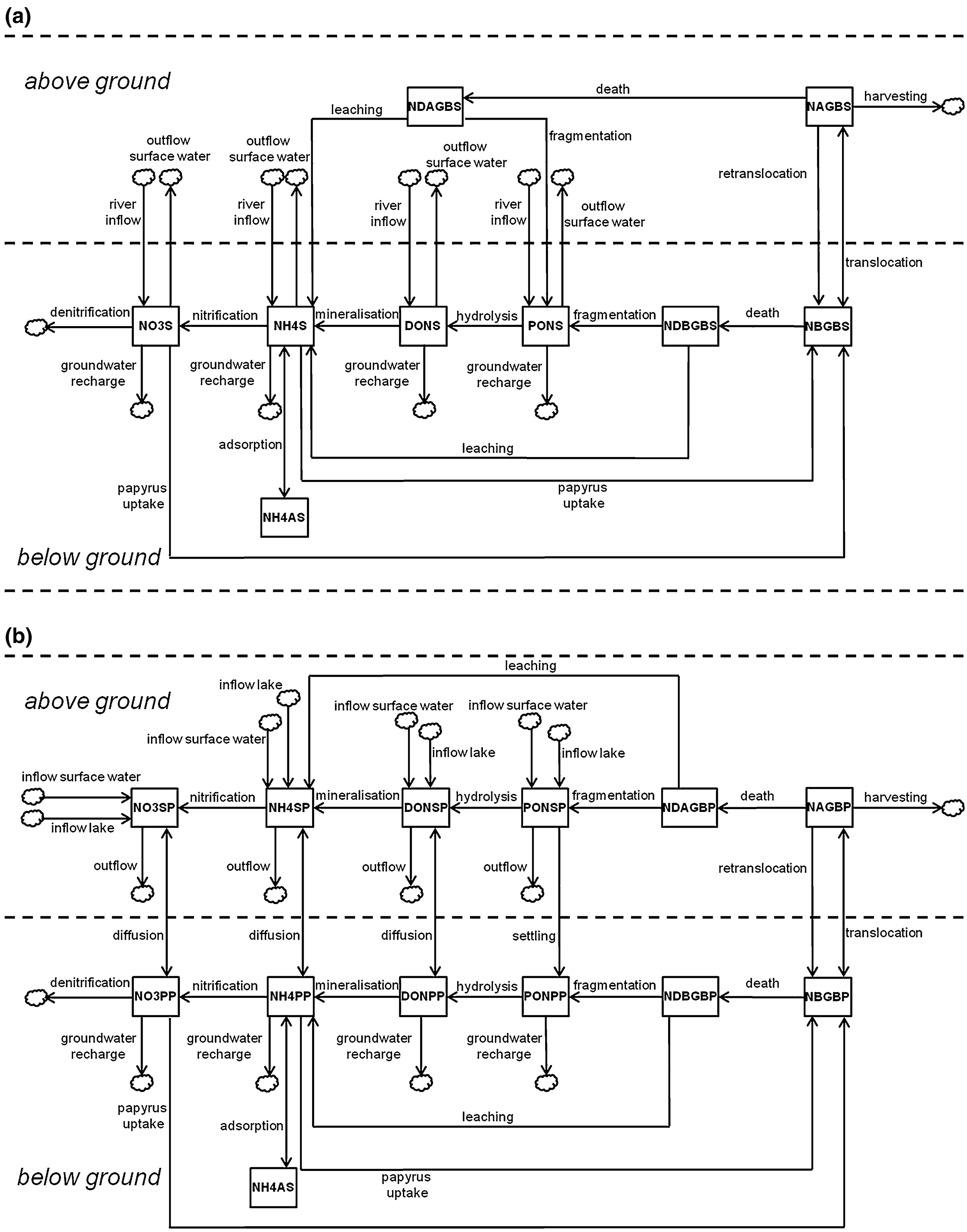

Fig. 4 Conceptual diagram of the nitrogen sub-model for the seasonally flooded zone (**a**) and permanently flooded zone (**b**) (names of state variables are explained in Table 1)

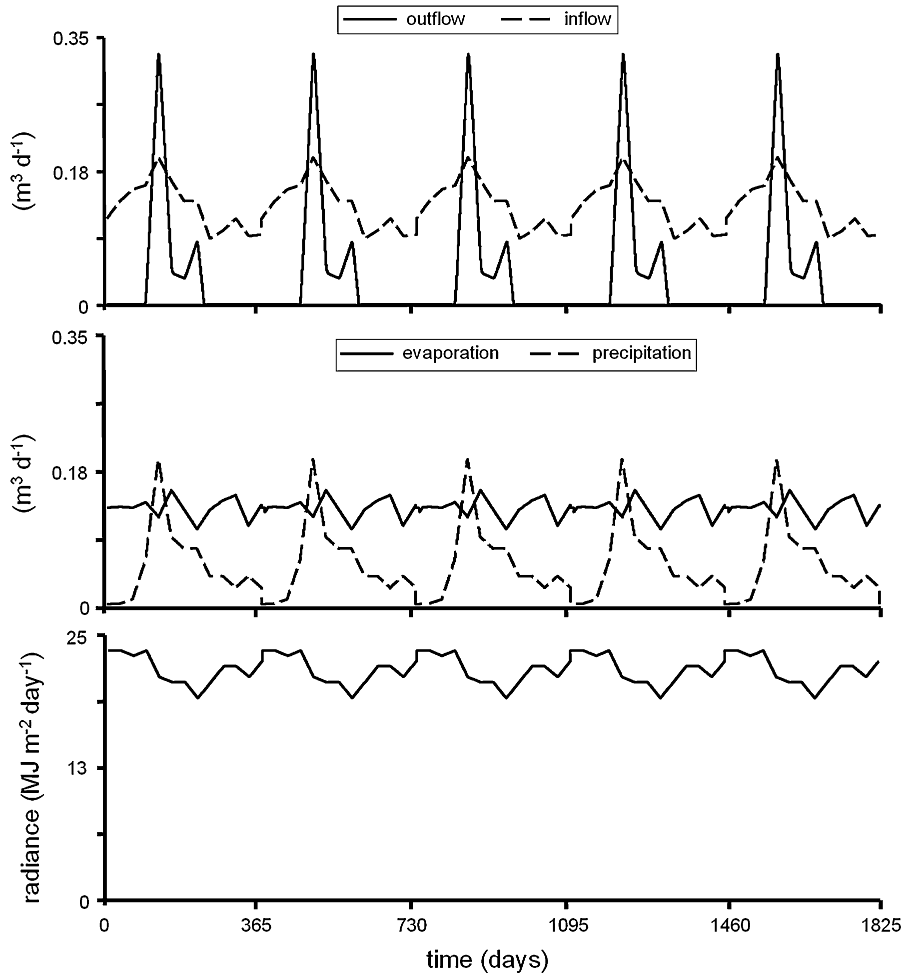

Fig. 5 River inflow in the S zone, outflow to the lake from the P zone, evaporation, precipitation and radiance

47, 60 and 61). Respiration was calculated assuming that maintenance respiration is proportional to biomass and that growth respiration was proportional to assimilation and translocation, as:

$$\begin{aligned}\text{Respiration} = {} & \text{maint\_coeff\_AGB} \times \text{CAGB} \\ & + \text{maint\_coeff\_BGB} \times \text{CBGB} \\ & + \text{growth\_coeff\_AGB} \times \text{assimilation} \\ & + \text{growth\_coeff\_BGB} \times \text{translocation})\end{aligned}$$

in which maint_coeff_AGB and maint_coeff_BGB are the maintenance respiration coefficients for aboveground and belowground biomass, respectively (/day), and growth_coeff_AGB and growth_coeff_BGB are the respiration coefficients for assimilation and translocation, respectively (−).

Both CAGB and CBGB were subject to death (flow to carbon in dead biomass), fragmentation (aboveground and belowground dead biomass being converted to particulate organic carbon in the sediment) and hydrolysis. All carbon processes were defined separately for the S and P-zones (Fig. 3a, b). In the S-zone, because of the short residence time (about 2 days) of the surface water, hydrolysis of particulate organic carbon was assumed to take place in the pore water only.

Nitrogen sub-models

The nitrogen sub-models (Fig. 4) express the same aboveground and belowground live and dead biomass compartments as the carbon model in terms of nitrogen.

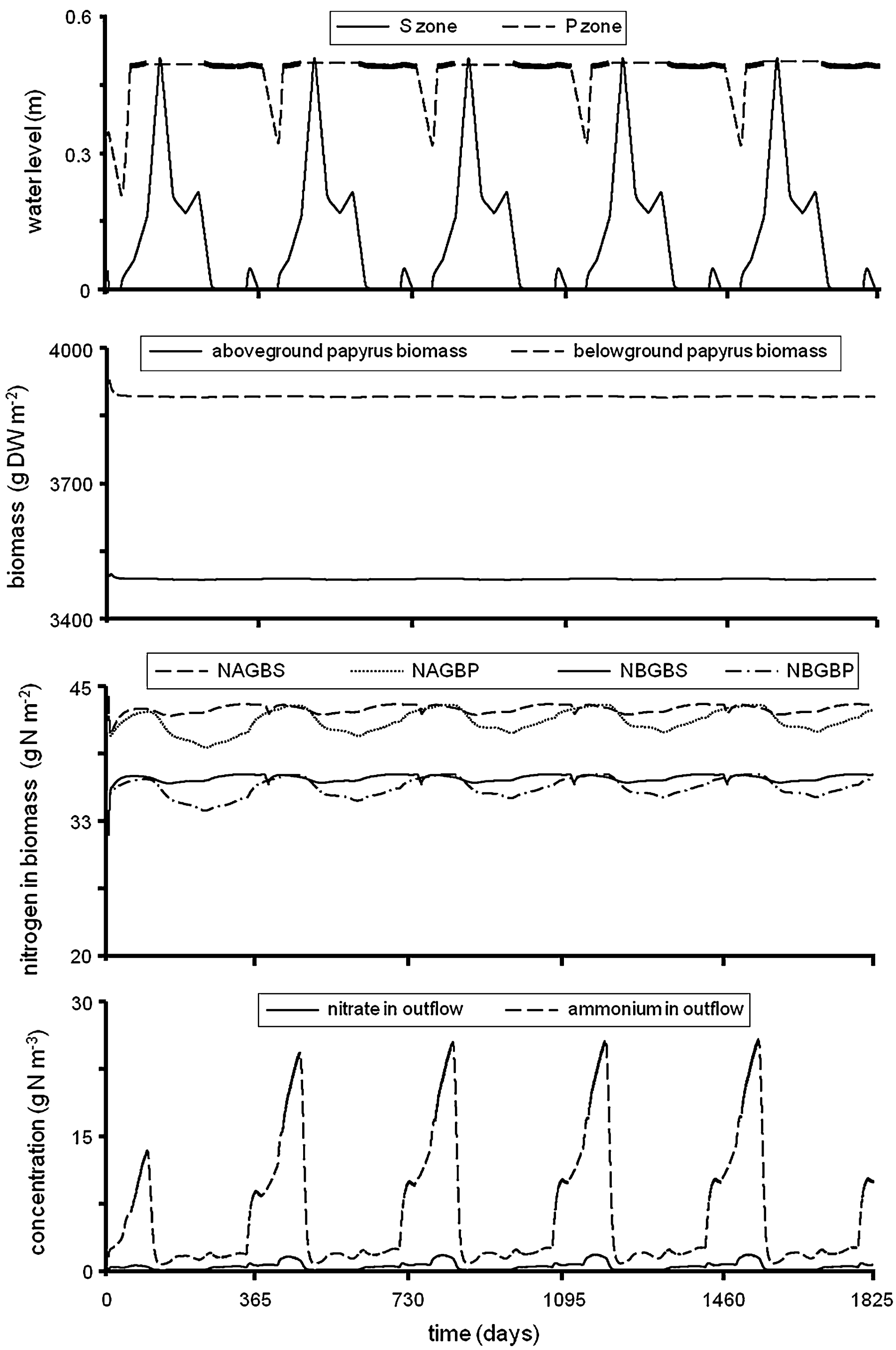

Fig. 6 Simulated water levels, papyrus biomass, nitrogen in papyrus biomass (NAGBS = nitrogen in aboveground biomass in S zone; NAGBP = nitrogen in aboveground biomass in P zone; NBGBS = nitrogen in belowground biomass in S zone; NBGBP = nitrogen in belowground biomass in P zone) and nitrate and ammonium concentrations in the outflow of the P zone

Added to these are the main components of the nitrogen cycle in the wetland. Nitrate and ammonium, originating from river to lake inflow as well as from the microbial breakdown of dead papyrus, are taken up by the belowground biomass, and then passed on to the aboveground biomass by translocation. Uptake rates (Eqs. 94, 100, 131 and 135) were related directly to CO_2-assimilation assuming a fixed C/N ratio in the papyrus biomass (Table 2). Nitrogen in dead biomass passes through fragmentation, hydrolysis, mineralisation and

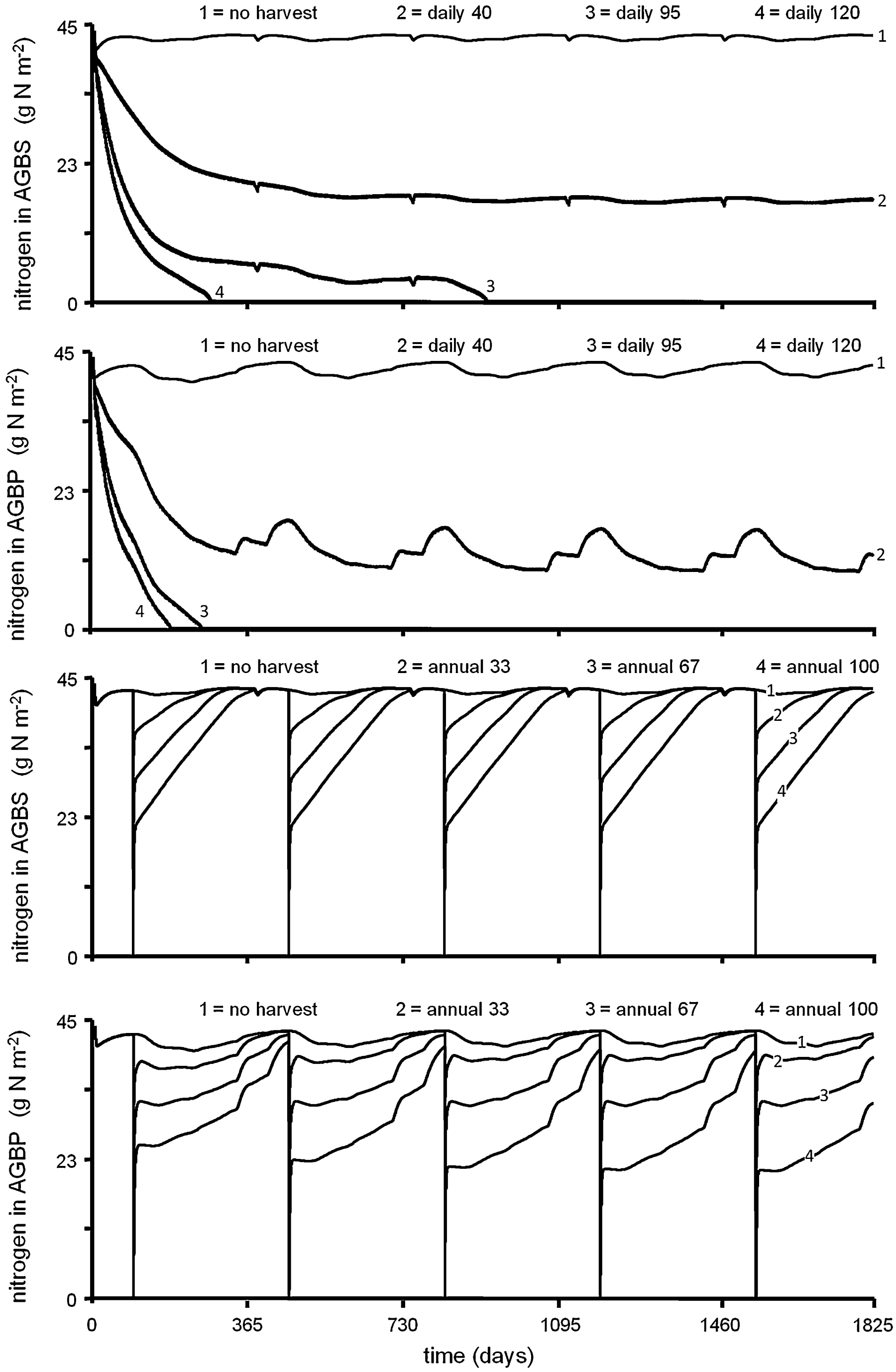

Fig. 7 Nitrogen in aboveground biomass under four daily harvesting scenarios: no harvest, daily 40 (40 g DW of papyrus), daily 95 (95 g DW of papyrus) and daily 120 (120 g DW of papyrus) and four annual harvesting scenarios: no harvest, annual 33 (33 % of aboveground biomass), annual 67 (67 % of aboveground biomass) and annual 100 (100 % of aboveground biomass) in the S zone and P zone respectively

nitrification. Nitrification (Eqs. 95, 123 and 132) and denitrification (Eqs. 98 and 129) were moderated by oxygen availability through the factor MODE. Ammonium adsorption to the soil (Eqs. 89 and 124) takes place when the NH_4 concentration is above 5 g N/m^2.

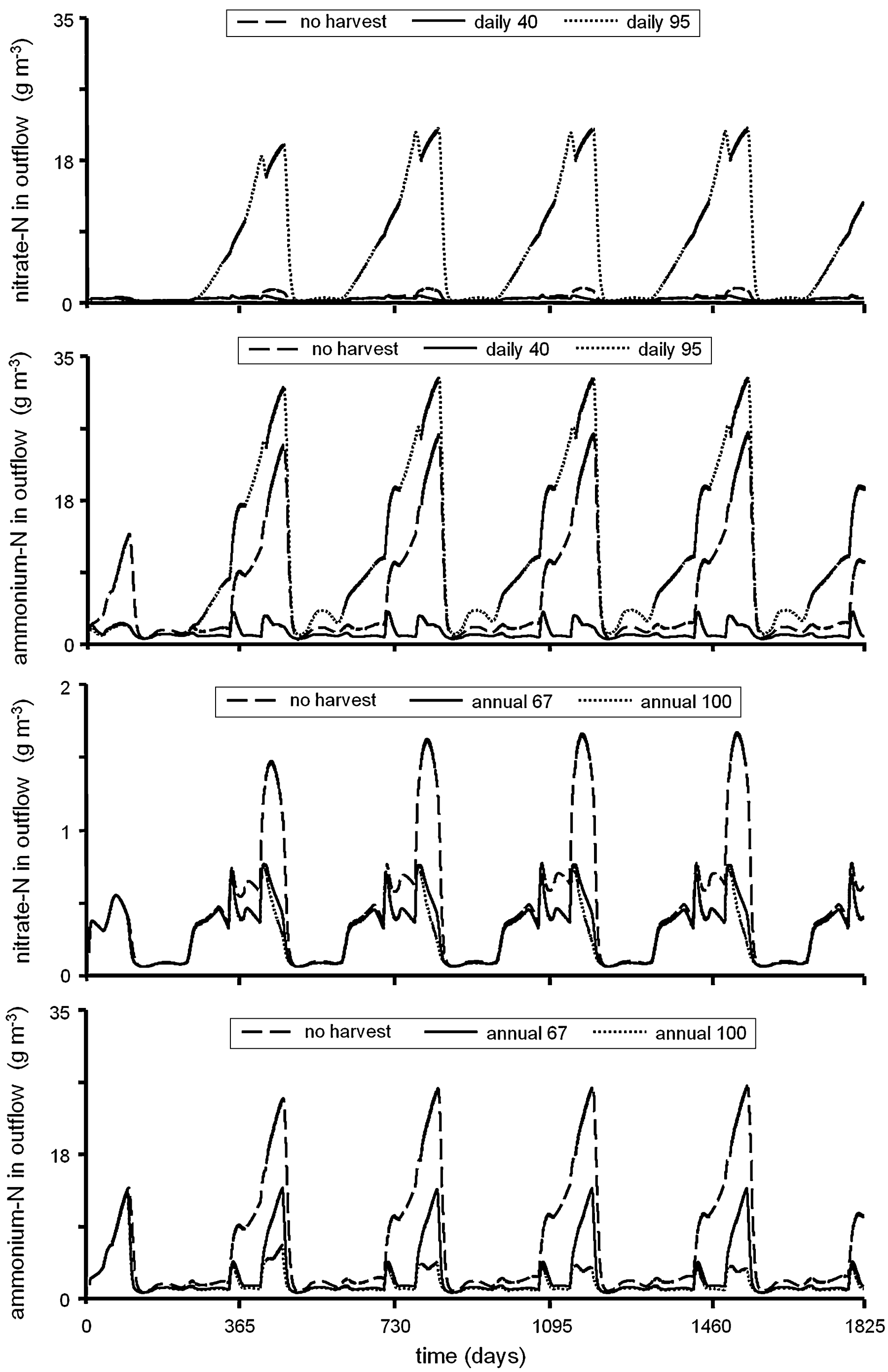

Fig. 8 Nitrate and ammonium in the outflow of the P zone under three daily harvesting scenarios: no harvest, daily 40 (40 g DW of papyrus) and daily 95 (95 g DW of papyrus) and three annual harvesting scenarios: no harvest, annual 67 (67 % of aboveground biomass) and annual 100 (100 % of aboveground biomass)

All nitrogen processes were defined separately for the S and P-zones. In the S-zone model, only belowground processes taking place in the pore water were modelled because surface water in this zone has a short residence time. Exchange of N between the aboveground and belowground layers in the P-zone takes place through diffusion, driven by concentration differences of soluble compounds (nitrate, ammonium

Table 3 Nitrogen budget for S zone and P zone over the fifth year without harvesting and with daily harvesting of 40, 95 or 120 g/m^2*d (DW)

	Compartment	N-flow									
		No harvest		No harvest		Daily 40		Daily 95		Daily 120	
		S (g N m^{-2} year^{-1})	P	S (% of N_{in})	P	S (% of N_{in})	P	S (% of N_{in})	P	S (% of N_{in})	P
N_{in}	PON	36.5	33.0	22	20	22	20	22	20	22	20
	DON	36.5	57.7	22	35	22	35	22	35	22	35
	DIN	91.3	75.5	56	45	56	45	56	45	56	45
N_{accum}	AGB	0	0	0	0	0	0	0	0	0	0
	BGB	0	0	0	0	0	0	0	0	0	0
	DAGB	19.0	18.7	12	11	4	3	−1	0	0	0
	DBGB	2.0	2.0	1	1	0	0	0	0	0	0
	PON	0.1	0.2	0	0	0	0	0	0	0	0
	DON	0.1	1.5	0	1	0	1	0	0	0	0
	DIN	0	0	0	0	0	0	0	0	0	0
	Adsorbed	0	0	0	0	0	0	0	0	0	0
N_{out}	PON	32.6	16.3	20	10	16	8	14	8	13	8
	DON	59.0	90.1	36	54	33	48	32	46	31	46
	DIN	51.0	37.2	31	22	2	7	53	43	53	43
	Denitrification	0.4	0.1	0	0	0	0	2	3	2	3
	Harvesting	0	0	0	0	45	33	0	0	0	0
N_{inflow}		164.3	166.2	100	100	100	100	100	100	100	100
$N_{outflow}$		142.6	143.6	87	86	51	64	98	97	98	97
N-retention	Total	21.7	22.6	13	14	49	36	2	3	2	3

Numbers are flows in g N/m^2 years (without harvesting) and in % of total N input into the wetland (all scenarios), for both S-zone and P-zone. N_{accum} is the net difference in a compartment between start and end of the year. N_{inflow} = N_{in} (PON+DON+DIN) and $N_{outflow}$ = N_{out} (PON+DON+DIN)

and dissolved organic nitrogen) and settling of particles (particulate organic nitrogen).

The uptake of ammonium and nitrate by papyrus depends on the carrying capacity for papyrus (max_AGB_biomass) and is limited by the concentration of ammonium and nitrate, respectively. This limitation was modelled with a Monod-type equation:

$$\text{NH4S\_uptake} = \text{max\_NH4\_uptake} \times \text{N\_papyrus\_S} \times \left(1 - \frac{\text{N\_papyrus\_S}}{\text{N\_max\_papyrus}}\right) \times \frac{\text{conc\_NH4S}}{(\text{conc\_NH4S} + \text{K\_NH4})}$$

in which max_NH4_uptake is the maximum uptake rate of ammonium by papyrus (/day), N_papyrus_S is the amount of nitrogen in above- and belowground biomass in the S zone (g/m^2), N_max_papyrus is the maximum amount of nitrogen stored in papyrus biomass (g/m^2), conc_NH4S is the ammonium concentration in the S zone (g N/m^3), and K_NH4 is a half saturation constant (g N/m^3).

N_max_papyrus was calculated based on literature values for nitrogen content in both above and belowground biomass, 0.013 and 0.008 g N/g DW respectively (Online Resource 1) and the maximum papyrus density in literature, 8,118 g DW/m^2 (Muthuri et al. 1989 and Jones and Muthuri 1997). Equations for nitrate uptake in the S zone (100) and ammonium and nitrate uptake in the P zone (131 and 135) are listed in Table 2.

Nitrogen retention and harvesting scenarios

Nitrogen retention (g N/m^2 year) was calculated as $(N_{inflow} - N_{outflow})/N_{inflow} * 100\%$ for the S and P-zones separately, in which N_{inflow} for the S-zone was the amount of nitrogen carried with inflow_S (44) in a year, and N_{inflow} for the P wetland was the sum

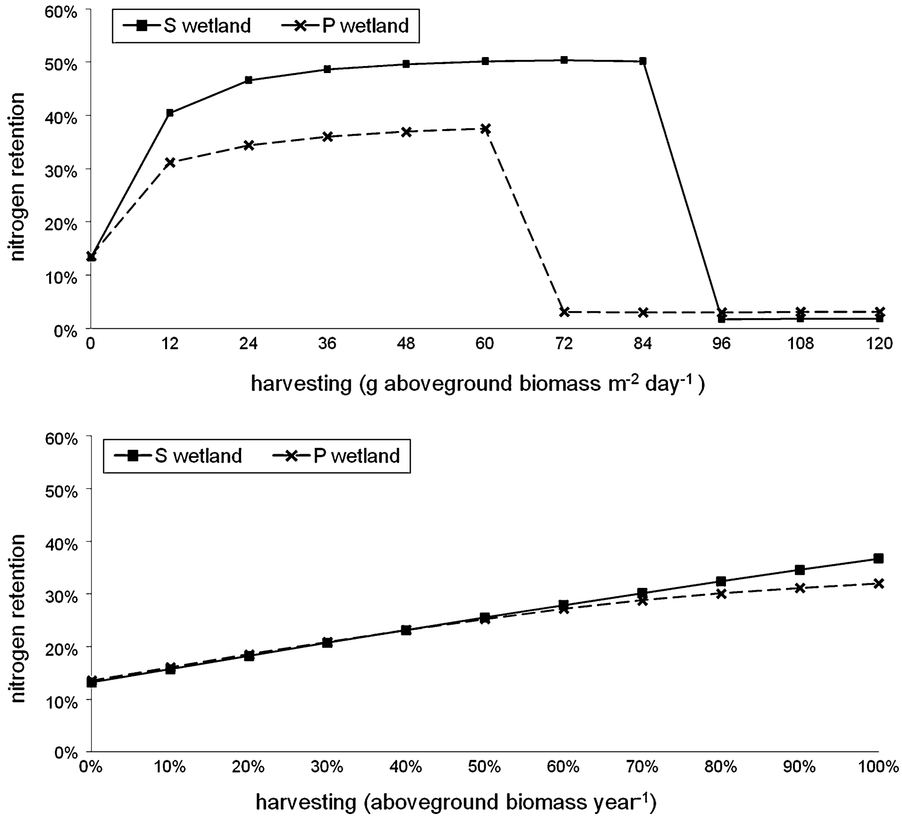

Fig. 9 Nitrogen retention in S zone and P zone under two harvesting scenarios: daily harvesting (*top*) and annual harvest at highest biomass density (*bottom*)

of the nitrogen in lake_inflow (36) and surface_water_flow (41). The $N_{outflow}$ of the S wetland was the sum of surface_water_flow (41) and recharge_S (45), and the $N_{outflow}$ of the P wetland was outflow (37) plus recharge_P (40). Retention was calculated over the 5th year when the system was observed to be stable.

Seven harvesting scenarios were defined: no harvest, daily 40 (daily harvest of 40 grams dry weight of aboveground papyrus biomass per square meter), daily 95 (95 grams of aboveground papyrus biomass), daily 120 (120 grams of aboveground papyrus biomass), annual 33 (33 % of the aboveground dry weight biomass, harvested annually at the 90th day of the year), annual 67 (67 % of the aboveground biomass) and annual 100 (100 % of the aboveground biomass).

Results

Water depth, water quality and papyrus growth

The water level in the S-zone (Fig. 6) showed two peaks coinciding with the two rainy seasons. The water level in the P-zone was always above 0.3 m, with the lowest level just before the start of the main rainy season. In the S-zone the wetland fell completely dry at the begin0 ning and the end of the year. Without harvesting, aboveground papyrus (Fig. 6) fluctuated between 3,480 and 3,485 g DW/m^2 within a year, with an initial value of 3,489 g DW/m^2 (Online Resource 1). Belowground biomass fluctuated between 3,890 and 3,893 g DW/m^2, after starting at a value of 3,928 g DW/m^2. Total biomass was around 7,375 g DW/m^2 (corresponding to 80 g N/m^2) for both S-zone (Fig. 6) and P-zone. Nitrogen in aboveground biomass (Fig. 6) was higher (41–43 g N/m^2) than in belowground biomass (35–37 g N/m^2). At the beginning of the year, before the start of the rainy season, the nitrogen in both aboveground and belowground biomass in the S-zone decreased and then increased again after the onset of the rains. Most of the year there was more nitrogen stored in biomass in the S-zone than in the P-zone. Nitrate and ammonium levels in the surface water of the P-zone (Fig. 6) increased during the period of the year when there was no outflow (Fig. 5) to 1.7–25 g N/m^3, respectively. During the period with outflow from the P-zone to the lake, the concentrations dropped to 0.5 g N/m^3 for nitrate and 3 g N/m^3 for ammonium.

Effect of harvesting on aboveground biomass

Figure 7 shows the nitrogen (in g N/m^2) in the aboveground parts of the papyrus in the S and P-zones with the seven harvesting scenarios. The amount of nitrogen stored in living aboveground papyrus decreased with increasing daily harvesting rates and stabilized over time. This implies that papyrus remained present in the wetland, but with a lower density than without harvesting. At a harvesting rate of 95 g/m^2 day, the system collapsed and the papyrus disappeared. According to the simulations this happened after two and a half year in the S zone and within a year in the P zone. The papyrus in the P zone collapsed earlier due to low nitrate and ammonium concentrations in the root zone (max 0.1 an 0.2 g N/m^3 respectively). With annual harvesting in the S-zone, the papyrus recovered to its original density even if all aboveground papyrus was harvested. The recovery after harvesting of more than 67 % took longer than half a year. For the P-zone, recovery took longer than in the S-zone again due to low nitrate and ammonium concentrations. The papyrus was not able recover to its original density if more than 67 % was harvested each year.

Effects of harvesting on outflow concentrations of nitrate and ammonium

The nitrate and ammonium concentrations in the surface water of the P-zone (Fig. 8), which is also the concentration of the outflow, increased during the period without outflow due to accumulation. During the period with outflow the concentrations dropped. Daily harvesting (daily 40) reduced both nitrate and ammonium concentrations, however when the harvesting rate increased (daily 95) the concentrations were even higher than without harvesting, with no dead biomass accumulation (Table 3). With annual harvesting, both nitrate and ammonium concentrations were lower as the amount harvested increased. Ammonium concentrations were higher than nitrate concentrations throughout.

Effects of harvesting on nitrogen retention

Figure 9 compares nitrogen retention in the S-zone and the P-zone. Under the daily harvesting scenario (daily harvesting of aboveground biomass), harvesting increased N-retention from 13 to 50 % for the S-zone and from 14 to 38 % for the P-zone. This is due to re-growth of the papyrus after harvesting. The difference between the S and P-zones is caused by nitrogen limitation in the P-zone. When daily harvesting is increased further, there is a sudden decrease in retention. This tipping point occurs between papyrus harvesting rates of 84 and 96 g/m^2 day in the S-zone and between 60 and 72 g/m^2 day in the P-zone. Beyond this point the amount harvested was bigger than the re-growth and therefore the papyrus is not able to recover and there was no aboveground biomass.

Nutrient retention without harvesting is mainly the accumulation of dead papyrus biomass (Table 3). Once the aboveground biomass is zero there was no longer accumulation of dead biomass and retention was only caused by denitrification (Table 3). Retention in the P-zone without aboveground biomass is higher than in the S zone (Fig. 9) because of denitrification (Table 3). The anaerobic conditions required for denitrification occur for a longer period of the year in the P-zone.

Figure 9 also shows the N-retention under annual harvesting, expressed as a percentage of the total aboveground biomass. In the S-zone, N-retention increased linearly, indicating that all the harvested papyrus grew back before the next harvest. In the P-zone, there was also a linear increase up to about 40 % of harvesting. For these harvesting rates, N-retention was slightly higher (about 1.5 g N/m^2 year) compared with the S-zone because of accumulation of dissolved organic nitrogen (Table 3). Above 40 % harvesting, nitrogen became limiting in the P-zone, leading to a smaller increase in retention. The papyrus was not able to grow back to the same density within a year.

Discussion

Simulated papyrus biomass density (7,375 g DW/m^2) was comparable with literature values of 6,945 g DW/m^2 given in Boar (2006) and of 7,775 g DW/m^2 in Jones and Muthuri (1997). Nitrogen in aboveground and belowground biomass was 41–43 and 35–37 g N/m^2, respectively, which compares well with values of 44 for aboveground and 31 g N/m^2 for belowground nitrogen measured in the field (Boar et al. 1999; Boar 2006). Nitrate and ammonium concentrations of 0.5 and 3 g N/m^3 in the outflow were also realistic (Gaudet 1979; Cózar et al. 2007). Field observations show that it takes 6–12 months for aboveground biomass to grow back from rhizomes to roots. In the model (S-zone), this was about 9 months (Fig. 7). The dataset used for calibration was compiled from different studies in Naivasha spread over an extended time period (1989–2006). While the model simulated the Naivasha papyrus system well, calibration and validation with field data from other papyrus wetlands is needed to confirm that the model predicts papyrus growth correctly within a range of hydrological and biogeochemical conditions.

Because of differences in hydrology, the nitrogen processes were modelled differently in the S and P-zones (Figs. 2, 4). Due to rapid flow of surface water to the P-zone and its short residence time (2 days) in relation to the rates of the processes in the surface water, in the S-zone only pore water processes were considered. In the P-zone, the residence time of surface water was longer and therefore both surface and pore water processes were included. During parts of the year with backflow from the lake instead of outflow (Fig. 4), there was an accumulation of dissolved nitrogen and, therefore, elevated concentrations in the P-zone surface water (Fig. 6). Nitrogen concentrations increased even further when the water level dropped temporarily because the evaporation was higher than the sum of all water inputs (Fig. 2).

Where possible, parameter values from published studies on papyrus vegetation of Lake Naivasha were used (see also Online Resource 1). Some constants were taken from the "parent" models (van der Peijl and Verhoeven 1999; van Dam et al. 2007; Table 2 and Online Resource 1). Further work on the model will include a sensitivity analysis to identify the parameters that influence the model outputs most and could be the focus of additional field or laboratory research.

Without harvesting, N-retention was between 13 and 14 % of N-input, equivalent to approximately 22 g N/m^2 year, similar to 21.5 g N/m^2 year estimated for a floating papyrus wetland (van Dam et al. 2007). The model results suggest that the major part of this nitrogen (19 g/m^2 year) accumulates in dead aboveground biomass and the remainder in dead belowground biomass, particulate and dissolved organic nitrogen (Table 3). Accumulated detritus may eventually be removed from the wetland by floods (van Dam et al. 2007). Nitrogen is removed permanently by denitrification, estimated in the model at 0.1–0.4 g N/m^2 year as a result of low nitrate concentrations. Based on model simulations, Mwanuzi et al. (2003) also concluded negligible denitrification in papyrus wetlands. Field measurements on denitrification in papyrus wetlands that can be used to verify model results are scarce.

The effect of harvesting on N-retention is positive. Harvesting reduces papyrus biomass and stimulates re-growth thus increasing nitrogen uptake. As the papyrus in the S-zone can grow back within a year, annual batch harvests, even up to 100 % of the *aboveground* papyrus, increase N-retention (Fig. 9b). According to the model simulations, the effect of daily harvesting on N-retention is positive up to a harvesting rate of about 90 and 70 g DW/m^2 for the S-zone and P-zone, respectively (Fig. 9a). The faster growth in the S-zone predicted by this mono-specific model does not take into account competition from other plant species that may occur under dry conditions (Rongoei et al. 2014). Above harvesting rates of about 90 and 70 g DW/m^2 for S and P-zone respectively, the system collapses (Figs. 7, 9) and N-retention is reduced to denitrification (Table 3).

The effects of hydrology and harvesting on N-retention show a strong interaction. Without harvesting, the difference between N-retention in the S-zone and the P-zone was small. With harvesting rates below 90 g/m^2 day aboveground biomass (Table 3 and Fig. 9), N-retention in the S-zone was higher than in the P-zone because of low nitrogen concentrations in the P-zone which limit re-growth (Fig. 8). These low concentrations occurred during the wet season, when water flowed from the P-zone to the lake and nitrogen could not accumulate to replenish the nitrogen taken up by the papyrus. Therefore when there was a net outflow to the lake, papyrus densities decreased with harvesting in the P zone (Fig. 5). With harvesting rates above 90 g/m^2 day, papyrus collapses and N-retention was only due to denitrification. Denitrification rates in the P-zone were higher because of anaerobic conditions throughout the year, whereas the S-zone is anaerobic only part of the year.

While harvesting contributes to N-retention at the wetland scale as it exports nitrogen from the wetland, at the basin scale it only contributes to N-retention if the harvested material is not decomposed within the same basin. As harvested papyrus is often used locally for construction, handicrafts and fish traps, it could be argued that the nitrogen is not exported from the basin.

For the model to contribute to better understanding of nutrient regulation function of papyrus wetlands the model needs further development. Gaudet (1975) showed that the N content of different papyrus organs (root, rhizome, culm and umbel) varies from 0.86 in the culm to 2.67 %DW in the rhizome. Consequently, the N content of a young, growing papyrus stand can be expected to change with the change in development stage of the plants. The current model, with a constant N content, could be improved by incorporating an allometric relationship between N content and biomass. A further improvement is the incorporation of phosphorus in the model. This would allow the estimation of P-retention in the papyrus wetland. P-retention is affected by harvesting (P content: 0.024–0.099 %DW in 10 different sites in Africa; Gaudet 1975), however, adsorption to the soil is more important in P retention (Kelderman et al. 2007). Including phosphorus will also allow the evaluation of N:P ratios in the plants and the effects of stoichiometry on nutrient cycling. As plants take up nutrients in proportions that maintain their optimal element ratio (Elser et al. 2010), variations in growth stages and vegetation harvesting may affect the N:P ratio of the outflow. This may have implications for the nutrient regulation function of papyrus wetlands and the water quality in the adjoining lake.

Acknowledgments This research was carried out within the framework of the EU-FP7-Wetwin project and the Ecolive and MaraFlows projects funded by the Dutch Ministry of Development Cooperation.

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