

# Phosphorus and nitrogen allocation in *Allium ursinum* on an alluvial floodplain (Eastern France). Is there an effect of flooding history?

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**Abstract** The change in phosphorus and nitrogen content in a common geophyte spring species, *Allium ursinum*, is studied in alluvial forests in relation to three flooding histories related to river regulation: (1) annually flooded, (2) unflooded for 30 years, and (3) unflooded for 200 years. Flood suppression leads to a reduction of available P soil content as well as decreasing the biomass and the amount of phosphorus in plants, but has no significant effect on N plant content. Plant N:P ratio increases with the suppression of floods and is primarily driven by soil N:P ratios, in turn markedly linked to the total nitrogen in the soil. We highlighted a lower nutrient accumulation in leaves during plant growth in unflooded forests. Overall, our results suggest that P was the main limiting factor in unflooded forests while nitrogen was the main limiting factor in annually flooded forests. Flood suppression strongly affects the morphology and nutrient uptake by *Allium ursinum* and thus nutrient cycling in riverine forests.

**Keywords** *Allium ursinum* · Flooding history · Nitrogen · Nutrient bioavailability · Phosphorus · Rhine

## Introduction

Hydrological regime is now considered as a key factor driving ecological functioning and biodiversity patterns of fluvial hydrosystems. Drastic changes in water flows, mostly related to hydraulic works in large rivers, lead to considerable changes in the floodplain biogeochemical cycles (Sanchez-Perez and Trémolières 2003; Lamers et al. 2006). Bioavailability of nutrients such as phosphorus and nitrogen is largely influenced by water level fluctuations (Pinay et al. 1993; Pinay and Trémolières 2000), and external inputs by overflows or by rising events of groundwater levels are known to enhance their availability (Baker et al. 2006; Lamers et al. 2006). On the other hand, floodplain areas are also considered as a sink for nutrients, and the groundwater connected to the river floodplain is usually nutrient-poor (Pinay et al. 1993; Lowrance et al. 1995; Takatert et al. 1999). So, in flooded forests, the control of nutrient bioavailability is rather complex. The water saturation of soils causes a decrease of redox potential that favours the P bioavailability (Fardeau and Dorioz 2000; Patrick et al. 1985; Shaw 1994), but leads to the removal of nitrate nitrogen by denitrification (Haycock and Pinay 1993; Lowrance et al. 1984; Lowrance et al. 1995; Pinay et al. 1993).

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And in calcareous soils, a high calcium carbonate content decreases P availability by precipitation and insolubility (Amer et al. 1991), but favours microbial activity and, in turn, litter decomposition and mineralisation, and thus nutrient disposal for plants (Badre 1996). While most studies of nutrient bioavailability matched up plant nutrient content with upland soil fertility (Aerts and Decaluwe 1994; Boerner 1984; Vitousek 1982), the importance of flooding in nutrient availability was widely highlighted (Ogden et al. 2007) but still remained controversial as some recent studies showed that flooding re-establishment had no effect on N and P bioavailability (Ogden et al. 2007; Sorrell et al. 2007).

Due to a relative low bioavailability, phosphorus is often considered as a limiting factor for plant growth, but it has been shown that floods in alluvial forest could compensate this low bioavailability especially in calcareous soils (Weiss and Trémolières 1993; Weiss et al. 1991). On the other hand, a clear N limitation was highlighted in pristine floodplain by Antheunisse et al. (2006), but they observed no limitation at all in regulated floodplains. In order to measure availability and limitation, the N:P plant ratio which indicates the balance between N and P is a useful tool, as an alternative to using N and P concentrations, to assess which nutrient limits biomass production (Güsewell and Koerselman 2002). Any potential limitation should influence plant nutrient resorption efficiency; indeed, resorption efficiency is an important mechanism of nutrient conservation for terrestrial plant species (Killingbeck 1996, Huang et al. 2007). Nutrient resorption allows plants to lower their dependence on soil nutrients, thereby influencing ecosystem-level processes such as litter decomposition and soil nutrient availability. Also, it has been shown that among different factors controlling nutrient resorption is the availability of plant resources such as nutrients, water or light (e.g. Covelo et al. 2008).

In this study, we used an ephemeral spring plant as a biological model to investigate the effect of floods on nutrient allocation. According to the vernal dam hypothesis (Anderson and Eickmeier 2000; Anderson and Eickmeier 1998), these short-lived plants accumulate and store nutrients in spring, and release nutrients later for growth of summer plants. We aim to examine the effect of flood suppression on the functioning of alluvial forests by quantifying the change in

nutrient availability as a result of flood suppression and to find which of N or P could be the limiting factor under these conditions. Next, we focus on plant mineral content and plant morphological descriptors to investigate the response of plants to change in nutrient availability. Finally, we want to estimate the amounts of nutrients accumulated (or loss) in plants during growth, and interpret the between-sites differences as possible responses to the dynamics of nutrients in floodplain forests.

## Materials and methods

### The studied species

*Allium ursinum* L. (*Alliaceae*) is a typical vernal geophyte species (Hérault and Honnay 2005) frequently occurring in alluvial forests, grows on nutrient-rich and well-moistened soils. Although growing in dense, almost pure stands, *Allium ursinum* is often irregularly distributed without any identifiable edaphical or microclimatical causes (Eggert 1992). The plant is sensitive both to water logging and to drought, and therefore its presence demonstrates that the environmental conditions in floodplains are well-balanced. *Allium ursinum* forms patches in which the adult plants are very dense but (uncommon in monospecific plant clusters) adult dominance does not suppress seedlings and juvenile individuals (Grime et al. 1988). *Allium ursinum*, therefore, seems to be a weak intra-specific but a strong inter-specific competitor, and it has been shown that *Allium ursinum* competes with other herbaceous plants via soil and volatile compounds which inhibit seed germination and plant growth (Djurdjevic et al. 2004). Its life history has been analysed as a model of polycarp plants, those reproduced by seeds. After falling on the soil, most seeds remain dormant for several years. Once germinated, more than 6 years are needed for juvenile plants to attain the dry matter threshold level for the production of inflorescences. Since flowering plants show a marked negative annual dry matter balance, most of them are not able to flower again the following year (Eggert 1992). With the same amount of carbon reserves, the formation of new bulbs results in a considerably higher number of new ramets than the production of seeds (Ernst 1979).

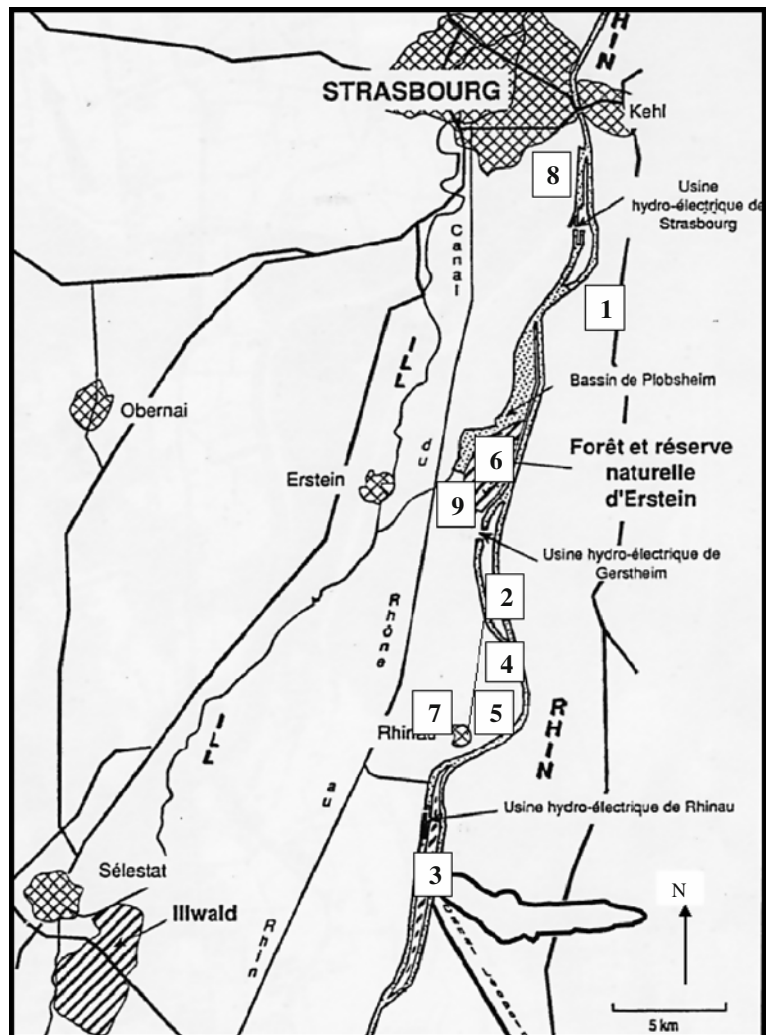
### The studied forests

The study was carried out in the Upper Rhine floodplain (Eastern France, 48°05'–48°35'N, 7°30'–7°46'E). The floodplain was composed of gravelly calcareous Rhine alluvium deposits to a maximum depth of 200 m. The dominant hydrological regime is characterised by summer high water and winter low water. The vegetation is composed of hardwood forests with oak, ash and elm as dominant species (Schnitzler 1995). The upper Rhine was subjected to a series of hydraulic management: regulation with embankment in the eighteenth and nineteenth centuries and canalisation in the twentieth century which has disconnected all the floodplain from the river

except annually flooded large islands created by the canalisation (Fig. 1).

We selected three types of sites which today have different hydrological conditions owing to this differential “flooding history”: one type is more or less annually flooded (on average 2 days per year for the period 1964–1990), a second one has been unflooded for 30 years (date of canalisation) and the last one has been unflooded for 200 years (since the embankment). Detailed characteristics of species composition and nutrient status are given in Trémolières et al. (1998). For a given type, three experimental forests were chosen, leading to a total of nine investigated forests, which are widely dispersed in the ancient floodplain and the Rhine islands (Fig. 1). The soils are named

**Fig. 1** Location of the nine studied sites in the upper Rhine floodplain (Eastern France): three forests are flooded annually (1, 2, 3), three have been unflooded for 30 years (4, 5, 6) and three for 200 years (7, 8, 9)



fluviosols (Fluvent A/C, USDA). They are sandy-gravelly calcareous soils (20–30% CaCO<sub>3</sub>, pH 7 to 8.5 at depth). Table 1 gives the averaged soil characteristics of the three types of forests. In each forest, three randomly-chosen quadrats were sampled.

### Sampling methods

*Allium ursinum* was sampled in a quadrat of 16 m<sup>2</sup> divided into four sectors. One sector was sampled at one of the three investigated growing stages (budding, flowering and beginning of senescence) while the remaining sector was used as a control throughout the experiment. In each sector, we collected all individuals from an area of 900 cm<sup>2</sup> in order to obtain population density and plant above- and below-ground biomass. Field studies were carried out from March to June 2006.

The soil was sampled on two dates, budding (end of March) and beginning of senescence (June) of *Allium* at three depths (0–5 cm, 20–25 cm and 40–45 cm). We considered that this depth-sampling was sufficient because the gravel level is close to the soil surface and the bulb reached a maximal depth of 30 cm (Ernst 1979).

### Laboratory analyses

Bulb and leaf lengths of 50 individuals per quadrat were measured in the field. After drying at laboratory temperature, the bulb and leaf masses were separately weighed and ground in a laboratory mill to pass through a 0.5-mm screen. Moisture was determined by drying for 24 h at 70°C. After an acid wet oxidation in HNO<sub>3</sub> and HClO<sub>4</sub>, phosphate was analysed with a micro flux auto-analyser. Total phosphorus was determined in the digests as phosphate after formation of a molybdate blue complex (APHA 1985). Total nitrogen was analysed as an elementary element by the apparatus ELEMENTAR, after powder combustion at 950°C and reduction into gases.

Soil cores of 5-cm thickness per horizon were taken. Total nitrogen was quantified by the Kjeldahl method after sulphuric digestion. Extractable phosphorus was measured according to the Joret & Hébert method (Joret and Hébert 1955), while ammonium and nitrate were analysed after extraction with KCl 1 mol l<sup>-1</sup>, ammonium by the indophenol blue method and nitrate by the cadmium reduction method (APHA 1985).

**Table 1** Flooding regime, soil and humus classification, soil texture and content of the nine floodplain forests investigated to assess phosphorus and nitrogen allocation in a spring ephemeral, *Allium ursinum*

Location	Rhine Islands	Daubensand forests	Dachsenkopf
	Rhinau-Gerstheim	Erstein Polder	Erstein polder
	Altenheim polder		Illkirch forest
Flooding regime	Annually flooded (2 days/year; 6 days in 2006)	Unflooded for 30 years since Rhine canalisation	Unflooded for 200 years since Rhine embankment
Soil	redoxic Fluviosol	Fluviosol with redoxic horizon	Typical Fluviosol
Humus	eutrophic hydromull	eutrophic mull	Mull-moder
<i>Soil texture</i>			
Clay (%)	18.9	38.4	25.7
Sand (%)	12	13	25.1
Silt (%)	69.1	48.6	49.2
<i>Soil content</i>			
Corg (%)	3.2	5.0	4.3
CaCO <sub>3</sub> (%)	30.6	24.8	28.1
Mg <sup>2+</sup> (meq/100 g)	1.7	1.38	1.6
Ca <sup>2+</sup> (meq/100 g)	42.7	40.5	43.5

## Statistical analyses

First, to avoid pseudo-replication problems (Hurlbert 1984), all data were averaged by forest. Quadrats within forests are true pseudo-replicates. In the following analyses, model residuals were always carefully checked for normality. In particular, we examined Cook's distances to ensure that no data point was disproportionately influential. Finally, to choose the best models including only the significant predictors, the Akaike Information Criterion was used in a stepwise algorithm alternating backwards and forwards in addition/exclusion of predictors (Legendre and Legendre 1998).

First, two-way analyses of variance with repeated measures (to properly test between- and within-forest effects) were used to test the effect of flooding history (FH) and of phenological period (PP) on soil nutrient content (NC).

$$NC_i = FH_i + PP_i + FH_i : PP_i + \varepsilon$$

where  $i$  is a given forest and  $\varepsilon$  the model residuals. Next, two-way analyses of variance with repeated measures were also used to test the effect of both FH and PP on plant vigour descriptors (VD, including both plant mineral content and plant morphological measures).

$$VD_i = FH_i + PP_i + FH_i : PP_i + \varepsilon$$

where  $i$  is a given forest and  $\varepsilon$  the model residuals. Spearman rank correlations were used to explore the relationships between N, P and N:P levels in plant (bulbs and leaves) and N, P and N:P levels in soils. Next, we used linear models to try to disentangle the simultaneous effect of FH, soil N/P ratios (SR) and plant PP on plant (bulbs or leaves) N/P ratios (PR):

$$PR_i = FH_i + PP_i + SR_i + FH_i : PP_i + \varepsilon$$

where  $i$  is a given forest and  $\varepsilon$  the model residuals. Finally, the amount of nutrients (N or P) accumulated or loss (ANA) in bulbs or in leaves during growth period was approximated using the following formula:

$$ANA_i = [(DW_{si} * C_{si}) - (DW_{bi} * C_{bi})] / (DW_{bi} * C_{bi})$$

where  $i$  is a given forest, DW the dry weight of bulbs or leaves, C the concentration of N or P at s (the beginning of senescence) and at b the budding stage. ANA was next used as response in four one-way analyses of variance performed to test the influence of FH on the amount of nutrients accumulated during growth.

## Results

### Inundation and nutrient bioavailability in soils

Flooding history was a significant factor of phosphorus variation in alluvial soils (Table 2). Indeed, exchangeable phosphorus in topsoil decreased from annually flooded forests to forests unflooded for 200 years. On the other hand, total nitrogen and nitrate increased significantly in the topsoil layers. Overflow is thus a major driver of soil nutrient contents in these alluvial forest systems.

### Biomass and nutrient plant content

Plants of annually flooded forests are remarkably more vigorous than other plants: they have higher leaves (and to a lesser extent bulbs) length and weight (Table 3). Total phosphorus in leaf and bulb is significantly higher in flooded forests but there is no relationship between N plant content and flooding history. There were significant differences in plant morphological descriptors with the sampling period: bulb and leaf length and weight increased with the ontogenetic stage whereas nutrient plant concentrations clearly decreased during the season. P and N accumulation, expressed as the amounts of nutrients accumulated during the growth season divided by the amounts present at the budding stage, was significantly greater in *Allium ursinum* leaves from flooded forests than in leaves from unflooded ones where nutrient accumulation was often negative (Table 4). In fact, there is a significant decrease in P and N leaf content in the sites unflooded for 200 years .

### N:P ratio

N:P leaf and bulb ratios varied from 3 to 60 throughout our data. However, mean values were between 3 and 26. We observed an excellent correlation between soil and plant N:P ratio (Table 6; Fig. 2). More specifically, it appears from Table 5 that the primary driver of N:P in plants was the total nitrogen in soil, even if nitrogen in bulbs and leaves was not correlated with nitrogen in soil (Table 5). Our results thus indicated that N:P ratios in bulbs and leaves were not directly linked to the flooding history (Table 6) but that flooding history drives N:P ratios in soil, in turn driving N:P ratios in plants (Fig. 2).

**Table 2** Assessment of the relative influence of forest flooding history (annually flooded, unflooded for 30 years, unflooded for 200 years) and of plant phenological period (budding and senescence stages) on N and P soil contents; two-way analyses of variance with interaction terms

	Forest flooding history					Plant phenological period				Interaction	
	<i>F</i>	<i>P</i>	0	30	200	<i>F</i>	<i>P</i>	Budding	Senescence	<i>F</i>	<i>P</i>
00–20 cm: [P exchangeable]	4.62	*	0.08±0.03	0.05±0.01	0.04±0.01	6.40	*	0.06±0.03	0.05±0.02	0.80	ns
20–40 cm: [P exchangeable]	1.25	ns	0.04±0.03	0.02±0.00	0.02±0.01	0.10	ns	0.03±0.02	0.03±0.02	0.68	ns
40–60 cm: [P exchangeable]	3.20	ns	0.02±0.01	0.01±0.00	0.01±0.00	0.05	ns	0.02±0.01	0.02±0.01	2.21	ns
00–20 cm: [N- NH <sub>4</sub> <sup>+</sup> ]kg ha <sup>-1</sup>	1.65	ns	15.5±8.8	25.2±11.9	19.2±8.2	11.66	*	25.6±10.4	14.3±5.8	0.22	ns
20–40 cm: [N- NH <sub>4</sub> <sup>+</sup> ] kg ha <sup>-1</sup>	0.61	ns	7.7±2.2	9.2±3.3	9.4±3.2	14.54	**	7.0±2.7	10.5±1.9	0.42	ns
40–60 cm: [N- NH <sub>4</sub> <sup>+</sup> ] kg ha <sup>-1</sup>	0.20	ns	3.7±1.9	4.4±2.9	4.0±1.4	6.43	*	3.1±1.7	5.0±2.1	3.26	ns
00–20 cm: [N- NO <sub>3</sub> <sup>-</sup> ] kg ha <sup>-1</sup>	4.73	*	11.3±2.7	15.2±1.2	13.5±1.9	3.90	ns	12.6±2.4	14.0±2.6	0.59	ns
20–40 cm: [N- NO <sub>3</sub> <sup>-</sup> ] kg ha <sup>-1</sup>	3.46	ns	13.1±4.6	16.4±6.0	19.8±7.1	35.81	***	11.9±3.8	21.0±4.8	0.23	ns
40–60 cm: [N- NO <sub>3</sub> <sup>-</sup> ] kg ha <sup>-1</sup>	4.45	ns	13.0±1.7	10.8±2.5	15.7±4.8	0.03	ns	13.3±3.0	13.0±3.5	0.29	ns
00–20 cm: Ntotal‰	5.80	*	2.8±0.4	4.0±0.7	4.1±0.6	2.53	ns	3.8±1.0	3.4±0.7	0.26	ns
20–40 cm: Ntotal‰	4.40	ns	2.0±0.1	2.1±0.3	2.8±0.5	0.40	ns	2.3±0.5	2.4±0.5	0.04	ns
40–60 cm: Ntotal‰	0.37	ns	1.2±0.1	1.2±0.3	1.3±0.3	3.79	ns	1.1±0.2	1.3±0.3	1.51	ns

0 Forests regularly flooded, 30 forests unflooded for 30 years, 200 forests unflooded for 200 years, [P exchangeable] ‰ (g kg<sup>-1</sup>)

ns Not significant, \*significant at the 0.05 level, \*\*significant at the 0.01 level, \*\*\*significant at the 0.001 level

## Discussion

### Inundation and nutrient bioavailability in soils

Roughly speaking, soil fertility depends on three drivers: inputs of minerals by rainfall, throughfall and recycling by throughfall and litter. In alluvial ecological systems, flooding event is an alternative factor in the

system (Trémolières et al. 1998). Our results show that overflows are an effective true source of phosphorus but not of nitrogen (Table 2). Moreover, nitrate and total nitrogen content in the soil increase with the duration of flooding suppression. This suggests that overflows boost the turn-over of organic matter in alluvial soils through P fertilisation which, in turn, decreases the nitrogen concentrations. It is well known

**Table 3** Assessment of the relative influence of forest flooding history (annually flooded, unflooded for 30 years, unflooded for 200 years) and of plant phenology (budding and senescence stages) on *Allium ursinum* mineral content and morphological measures; two-way analyses of variance with interaction terms

	<i>F</i>	<i>P</i>	Forest flooding history			<i>F</i>	<i>P</i>	Plant phenological period		Senescence	Interaction	
			0	30	200			Budding	Flowering		<i>F</i>	<i>P</i>
Density (m <sup>-2</sup> )	0.16	ns	84.0±99.0	78.9±43.2	100.8±67.5	14.44	***	118.8±75.0	120.7±63.1	24.2±8.1	1.18	ns
Bulb length (cm)	3.49	ns	2.55±1.25	1.92±0.79	1.47±0.37	16.35	***	1.79±0.44	1.52±0.43	2.64±1.36	4.92	*
Leaf length (cm)	5.71	*	23.3±9.8	15.8±5.4	13.6±4.1	85.58	***	11.3±3.9	17.7±3.6	23.8±9.2	9.63	***
Bulb dry weight (g)	3.28	ns	0.21±0.27	0.12±0.12	0.07±0.06	15.25	***	0.04±0.02	0.08±0.05	0.28±0.22	2.01	ns
Leaf dry weight (g)	4.68	*	0.15±0.15	0.06±0.04	0.03±0.02	6.59	*	0.04±0.03	0.08±0.06	0.13±0.15	3.75	*
P bulbs (‰)	5.31	*	1.69±1.01	0.89±0.44	0.95±0.54	24.91	***	1.79±0.95	0.71±0.27	1.03±0.55	1.76	ns
P leaves (‰)	5.52	*	2.66±1.03	1.87±0.83	1.88±0.93	82.2	***	3.21±0.73	1.75±0.44	1.45±0.68	0.5	ns
N bulbs (%)	3.35	ns	1.74±1.03	1.45±0.75	1.39±0.67	57.80	***	2.29±0.67	1.33±0.69	0.94±0.26	1.50	ns
N leaves (%)	2.35	ns	3.7±1.9	3.6±2.1	3.3±1.7	127.21	***	5.40±1.53	3.30±1.25	1.96±0.28	8.44	**

0 Forests regularly flooded, 30 forests unflooded for 30 years, 200 forests unflooded for 200 years

ns Not significant, \*significant at the 0.05 level, \*\*significant at the 0.01 level, \*\*\*significant at the 0.001 level

**Table 4** Effect of forest flooding history (annually flooded, unflooded for 30 years, unflooded for 200 years) on the percentage of N and P accumulation (positive) or loss (negative)in bulbs and leaves of *Allium ursinum* plants during the growth period, one way analyses of variance

	Flooding History			Model	
	0	30	200	F	P
P leaves	164.5±29.8%	1.8±50.9%	-48.1±11.4%	30.8	***
P bulbs	443.3±253.6%	318.8±277.9%	94.0±82.1%	1.9	ns
N leaves	74.4±32.9%	-39.6±16.6%	-53.0±14.7%	28.0	***
N bulbs	187.7±191.0%	189.1±179.4%	63.8±81.5%	0.6	ns

0 Forests regularly flooded, 30 forests unflooded for 30 years, 200 forests unflooded for 200 years

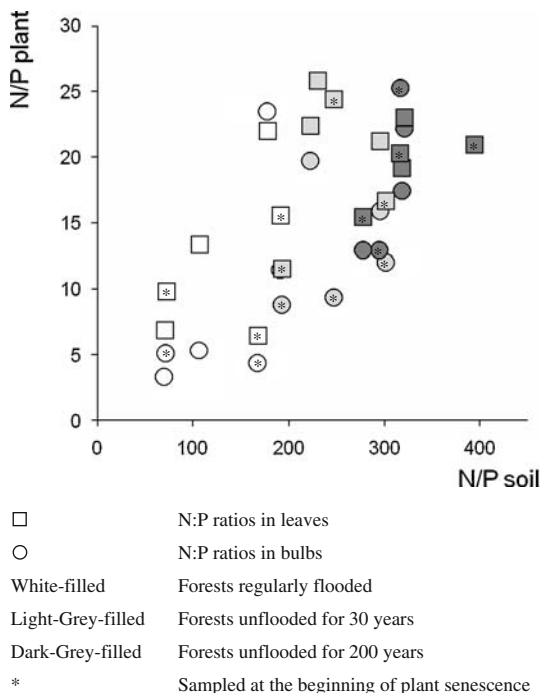
ns Not significant, \*\*significant at the 0.01 level

that nitrate is actively produced in flooded as well as in unflooded forests (Sanchez-Perez and Trémolières 2003; Takatert et al. 1999). However, denitrification is less efficient in unflooded than in flooded forest soils which could explain the higher nitrate content in unflooded soils (Forshay and Stanley 2005; Rutherford and Nguyen 2004). This suggests that both drivers of soil fertility elements are strongly linked to the flood-

ing regime, with each flood pulse driving element production, inputs or removal (Mitsch et al. 2005; Ogden et al. 2007).

#### Biomass and nutrient plant content

Our data clearly suggest a very close link between individual biomass and flooding history, as the leaf and, to a lesser extent, bulb lengths and weights are higher in annually flooded sites. Plainly, this observation was made at 'equivalent' plant densities, given that the latter does not depend on the forest flooding history (Table 3). Many studies have shown a relationship between soil nutrient richness and nutrient content in plants (Boerner 1984; Vitousek 1982). The relationship between fertility of soil enhanced in flooded sites and tissue P concentrations is well established in accordance with Demars and Boerner (1997) and Van Oorschot et al. (1997) in neutral or acid soil conditions. In our study, we made a hypothesis a priori that the contribution of flood inputs compensates a possible deficiency in P due to insolubility in calcareous soils (Amer et al. 1991). Indeed, the P leaf content is always higher in the flooded sites than in the unflooded ones (Table 3), highlighting the importance of floods. Moreover, there is a better correlation between bulb and soil P content than between leaves and soil P content (Table 5), which leads us to conclude that there is a good linkage of P in bulbs with P bioavailability in soil, which is in turn linked to flooding history (Table 2). These results are thus partly contradictory to the results of Gusewell and Koerselman (2002) who showed that there is no relationship between nutrient concentrations in plants and nutrient availability in flooded soils. We need to acknowledge, however, that N content in plants is not

**Fig. 2** Relative effect of N:P ratios in soils, flooding history (annually flooded, unflooded for 30 years, unflooded for 200 years) and plant phenological period (budding and senescence stages) on N:P ratio in bulbs and leaves of the spring ephemeral *Allium ursinum* in nine floodplain forests

**Table 5** Spearman rank correlation tests between N, P contents, N:P ratio in *Allium ursinum* plants and N, P contents, N:P in forest top soils

<i>Allium ursinum</i> plants	Forest soils (0–20 cm)		
	P exchangeable	[N-NO <sub>3</sub> -]	Ntot
P bulb	0.57**		
P leaf	0.45*		
N bulb		-0.24 ns	0.04 ns
N leaf		-0.34 ns	-0.01 ns
N:P bulb	-0.51*	-0.01 ns	0.65 ***
N:P leaf	-0.34ns	0.26 ns	0.54 **

ns Not significant, \*significant at the 0.05 level, \*\*significant at the 0.01 level, \*\*\*significant at the 0.001 level

related to flood history, and that there is no relationship between N plant and N soil (Table 5), while nitrate in soil significantly increases with the suppression of floods (Table 2), suggesting that environmental factors, such as divergent soil water supply driven by flooding history, can influence N use by plants (Yuan and Li 2007). This absence of a correlation may also indicate either that there is another factor which controls the N bioavailability in soils or that N content in soil highly fluctuates over a vegetation season, and that when there is a deficit in soil, *Allium* could use preferentially nitrogen stored in bulb.

#### What is the limiting factor?

N:P ratio gives an indication of the type of nutrient limitation, as underlined by Güsewell and Koerselman (2002). Koerselman and Meuleman (1996) proposed an interval of 14–16 for a well-balanced N:P ratio. This means that when N:P ratio is less than 14 nitrogen is limiting and when N:P ratio is superior to 16 it is phosphorus that is limiting. Van Oorschot (1994) and later Güsewell (2004) gave a threshold of 20 for this ratio above which P is a true limiting factor. In our study, plant N:P ratios vary between 3 and 27. The lowest ratios were observed in the flooded sites (Fig. 2), suggesting again that P is not the limiting factor in regularly flooded forests. However, it cannot be excluded that P storage and/or recycling in soils are not sufficient for phosphorus nutrition in unflooded forests. This may explain why P was less accumulated in bulbs and leaves during growth in unflooded forests (Table 4). Nitrogen seems to be the limiting factor in

the flooded sites as has been shown by Sorrell et al. (2007) and Antheunisse et al. (2006), probably due to the nitrogen removal by denitrification which commonly occurs in saturated soils (Rutherford and Nguyen 2004). Indeed, we have shown that bulb and leaf N:P ratios are highly correlated to total nitrogen in soils and not to soil phosphorus (Table 5).

#### Is there a specific role for spring ephemerals in mineral recycling?

The observed nutrient contents in *Allium ursinum* are close to those measured in other alluvial systems (Klimo 1985) or in riverine forested wetlands (Lugo et al. 1990), but significantly higher than those measured by Van Oorschot et al. (1997) in episodically flooded sectors, and surprisingly lower than those measured in *Allium* growing in a beech woodland (Jandl et al. 1997). In unflooded sites, leaf nutrient contents are clearly lower at the end of spring than at the beginning of spring (negative accumulation in Table 4). We suggest that this phenomenon could be related to some mechanisms of nutrient reallocation towards the plant bulb. In early spring, *Allium* grows in an open forest where light transmission is maximal, which explains the relatively high leaf nutrient contents (Anderson and Eickmeier 1998). On average, *Allium* stores 2.9 kg P ha<sup>-1</sup> in the poorer forests and 7.2 kg P ha<sup>-1</sup> in the flooded ones, and from 50 to 89 kg N ha<sup>-1</sup> during the study period (with a biomass of, respectively, 103 g m<sup>-2</sup> and 165 g m<sup>-2</sup>), which underlines the ecological role of vernal ephemeral herbs in nutrient storage (Tessier and Raynal 2003). After full leaf development, there could be a reallocation from leaves to bulbs within the plant, which explains the leaf nutrient decrease in the most

**Table 6** Prediction of N/P ratios in bulbs and leaves of *Allium ursinum* plants by flooding history, phenological periods and soil N/P ratios

N/P ratios	Predictors	Wald Statistic	P
Bulbs	Soil N:P	12.73	***
	Phenological period	5.14	*
Leaves	Soil N:P	12.24	***
	Phenological period	5.03	*

Linear models with stepwise procedures of variable selection based on Akaike's Information Criterion

\*Significant at the 0.05 level, \*\*\*significant at the 0.001 level

unflooded sites. Plants finally only release about half of the plant initial content in N and P after leaf senescence (Table 4). This behaviour is often observed for N and P chemical elements whereas other nutrients (Ca, for example) increase in leaves during the growing season (Moorhead and McArthur 1996). This contributes to P and N accumulation in the remaining living plants and avoids excessive loss by infiltration before the beginning of the true vegetative season in early summer. In contrast, there is a P and N accumulation in leaf in flooded sites (Table 4), and a large part of the nutrients can be released at leaf senescence. *Allium* thus contributes to an economy of nutrients during its whole life span in unflooded sites and to an efficient supply of nutrients to summer growth of trees in flooded sites. Therefore, the subcycle of nutrient turnover in *Allium* would not always be synchronous with nutrient cycles of trees, and the other sources of nutrient should be considered, such as lateral nutrient fluxes (Jandl et al. 1997), in order to explain high mineral content and high production.

## Conclusion

Our results showed firstly that flooding history greatly influences soil nutrient content in alluvial forest ecosystems. Secondly, plant biomass and phosphorus content are significantly linked to flooding history whereas plant density and N plant content are not. The ratio plant N:P is linked to soil N:P and particularly linked to total nitrogen in soil. Nitrogen appears thus to be the main limiting factor in flooded forests while unflooded forest systems were more limited by phosphorus availability. Floods contribute to P supply which enriches the plant, and explains the lower P accumulation in leaves during plant growth in unflooded forests. On the other hand, the absence of a correlation between N plant content and flooding is probably due to high levels of nitrogen transformation, to variations of availability in alluvial zones, to the removal by denitrification which leads to a possible deficiency in flooded zones and to the production from organic matter decomposition and mineralisation in unflooded zones (and in flooded zones only in dry periods). This suggests that the interaction between N content in plant and flooding seems rather complex. Depending on flooding history, the studied species, *Allium ursinum*, probably like other geophyte spring species, contributes to the storing or recycling of

nutrients at leaf senescence in June when other ligneous and herbaceous species are in full growth, and thus contributes to the minerals' annual cycle in alluvial forests.

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