Chapter 11
Biological Phosphorus Cycling in Grasslands: Interactions with Nitrogen

Claire Jouany, Pablo Cruz, Tanguy Daufresne, and Michel Duru

11.1 Introduction

Grassland ecosystems offer the opportunity to exploit several pathways in the phosphorus (P) cycle because biological as well as geochemical processes occur on different scales in the soil–plant system. We still need to improve our knowledge of these processes because accurate management of mineral resources becomes a priority when developing sustainable herbage production systems where economic and environmental issues are the main considerations (Ehlert et al. 2003; Abbot and Murphy 2003; Marriot et al. 2004). In this context, accurate P management within farming systems based on grass production is an important goal because P is often growth-limiting (Elser et al. 2007).

For cultivated grasslands, where appropriate P nutrition is required for optimizing forage production, the aim is to meet crop needs, which are largely determined by the level of N supplied from soil reserves and/or organic or mineral fertilizers. This amount varies greatly according to the site and the function of the grassland in the system (Bélanger et al. 1989; Schellberg et al. 1999; Griffin et al. 2002).

In natural grasslands in the absence of deliberate anthropic inputs, biological cycling is a major process to consider in order to understand the relationships between grassland P fertility and species richness. Grassland management for nature conservation purposes requires the maintenance of P-limited ecosystems because long-term high P availability is an obstacle to the restoration of natural grassland (Janssens et al. 1998; Critchley et al. 2002; McCrea et al. 2004; Wassen et al. 2005). This is important in places where the effect of atmospheric N deposition on species diversity is directly related to P availability (Limpens et al. 2004). Conservation practices recommend soil fertility reduction, principally through soil phosphate mining, in order to promote and sustain species-rich vegetation.

C. Jouany (✉), P. Cruz, and M. Duru
INRA-UMR AGIR, Chemin de Borde Rouge, BP 52627, 31326 Castanet-Tolosan Cedex, France
e-mail: cjouany@toulouse.inra.fr

T. Daufresne
INRA-CEFS, Chemin de Borde Rouge, BP 52627, 31326 Castanet-Tolosan Cedex, France

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Exhaustion of P reserves is achieved by forcing the grassland to produce biomass by means of a high N supply (Olde Venterink et al. 2001; Fagan et al. 2008).

11.1.1 P Cycle in Grassland Ecosystems

A schematic representation of the P cycle is given in Fig. 11.1. In grassland soils, the total concentration of P ranges between 200 and 1,100 mg kg^{-1} soil according to soil age (Walker and Adams 1958). Larger stocks are found in poorly developed young soils whereas the lowest concentrations occur in highly weathered ones (Lambers et al. 2008). As expected, P is present in both mineral and organic forms, whose relative contribution to the total stock varies between 20% and 90% (Fig. 11.1). P cycling is controlled simultaneously by geochemical and biological processes (Frossard et al. 1995), unlike the N cycle, which is largely controlled by biological processes. The total organic P concentration in grassland soils is not related to the total stock, but is a direct function of total organic carbon and N concentration (Walker and Adams 1958).

P concentration in aboveground biomass is commonly reported to vary between 1 and 5 mg g^{-1} dry matter according to the growth stage: major nutrient concentrations decrease with biomass accumulation as a consequence of dilution with growth (Lemaire and Gastal 1997; Duru and Ducrocq 1997). For grass swards, the

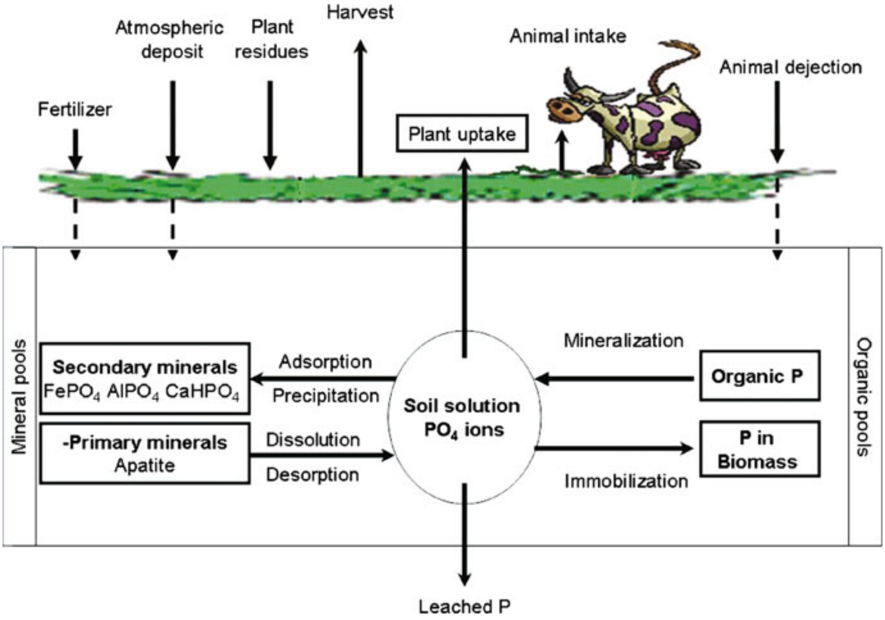

Fig. 11.1 Schematic presentation of the P cycle in a grassland ecosystem

P concentration decrease is a linear function of the sward N concentration (Duru and Thélier-Huché 1997). In cultivated grasslands, the intensity of the P flux leaving the system (output) is a direct function of the N management regime (Stroia et al. 2007; Watson and Matthews 2008). According to the methods of defoliation (cutting for hay or grazing) and fertilization, P balances on a field scale can differ considerably, from a negative balance where large P exports are not counterbalanced by fertilization, to a large surplus in over-fertilized grasslands (Stroia et al. 2007), which can represent important sources of P to surface runoff waters (Schärer et al. 2007). In natural grassland, fluxes of P are lower and are directly controlled by plant and animal residues, which decompose on the soil surface. Organic matter inputs result in very uneven nutrient availability (Güsewell et al. 2005) and, consequently, vegetation dynamics (Gillet et al. 2010).

In both fertilized and natural grassland ecosystems these processes lead to P accumulation in surface horizons due to the absence of ploughing and the low mobility of P ions. This results in a vertical gradient in the distribution of plant-available P down the soil profile and, consequently, a preferential localization of roots in the upper soil layers (Jobbágy and Jackson 2001).

11.1.2 Aims of the Chapter

Section 11.1.1 explains the complexity of soil–plant interactions in grassland ecosystems and highlights the importance of studying biological P cycling in relation with that of N. In order to discuss this, the chapter relies on several case studies that take advantage of original approaches developed by both agronomists and ecologists. They illustrate the interactions existing between N and P and their effects on ecosystem functioning. First, the nutrition index approach, based on nutrient dilution in the process of biomass accumulation, is presented (Sect. 11.2.2). This formalism, developed by agronomists, makes it possible to evaluate the relative response of biomass production in grassland in relation to changes in nutritional status (N and P). In parallel, the functional characterization of grassland vegetation from plant functional type (PFT) definition will be presented (Sect. 11.3.1.1). This relies on the fact that grassland communities may contain a wide diversity of species that influence nutrient biological cycling and regulate the biogeochemical cycle of nutrients. Finally, the effect of grazing herbivores on the biogeochemical cycle of major elements is addressed (Sect. 11.4).

11.2 Direct N–P Interactions in Grasslands

11.2.1 Influence of N–P Interaction on Grassland Production

N–P interaction is a major process that controls photosynthetic production in ecosystems. In a recent meta-analysis based on an exhaustive survey, Elser et al.

(2007) demonstrated that combined N and P enrichment produce similarly strong synergistic effects in all habitats, whether terrestrial, freshwater or marine. In agro-ecosystems, similar results are frequently reported for crops as well as grasslands (Aulack and Malhi 2005; Bélanger et al. 1989; Loeppky et al. 1999), or rangelands (Snyman 2002). These interactions do not always occur; they depend on annual weather conditions, because soil nutrient availability is controlled by water supply. N nutrition can be limited due to excessive rain and loss by leaching or low soil water availability, which limits N absorption (Mills et al. 2009). For P, low water supply limits P diffusion at the root interface and absorption by plants (Hinsinger 1998). Fertilization experiments conducted since 1999 on grassland with low soil P availability in Angladure (Ercé, French Pyrenees) revealed a significant positive N–P interaction (Stroia 2007). Four treatments were tested: control, +N, +P and +NP. N and P were added at the beginning of the vegetation period; extra N was supplied for the second cycle. An interaction for total annual dry matter yield (DMY) was observed in 10 years out of 11; when it occurred, its magnitude varied as shown in Table 11.1. The interaction appears to be more frequent for the first growth cycle and is occasionally found for the second or the autumn regrowth in wet years; however, it is difficult to identify the exact role of N and P in that interaction.

11.2.2 Analysis of N–P Interaction Using the Nutrient Index Approach

11.2.2.1 The Plant Nutrient Index Approach

This approach, developed by agronomists, relies on the nutrient dilution that takes place during biomass accumulation. The ratio of structural (low N concentration) to non-structural (metabolic tissue of high N concentration) tissue increases as biomass accumulates throughout regrowth (Lemaire and Gastal 1997). For grass-dominated swards, the decline in N concentration with biomass accumulation follows a curve with the following form (Fig. 11.2): $N_{\text{critical}}\ (\%) = 4.8 \times \text{DM}^{-0.32}$, where DM is accumulated dry matter (Lemaire et al. 1989). This critical N curve gives the minimum N concentration for maximum growth for different levels of biomass accumulation in swards, and can be used for diagnosing nutrient status. For a given sward biomass, the N nutrition index (Ni) is defined as the ratio (expressed as a percentage) of measured N concentration (N_{act}) to its corresponding optimum value obtained for identical biomass from the critical N curve (N_{c}) (Lemaire et al. 1989). This approach has been successfully applied to diagnose the N nutritional status of the different components in mixed cropping systems (Cruz and Soussana 1997) and grassland (Duru et al. 1997). A similar approach was later developed for major nutrients: Duru and Thélier-Huché (1997) demonstrated that for P there is no single critical P curve as found for N, since the variation in optimum P

Table 11.1 Average total annual dry matter yield response to N, P and NP

Treatments	Year										
	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Control	11.6 ± 1.2	11.3 ± 0.4	10.1 ± 1.9	8 ± 0.9	7.7 ± 2	4.9 ± 1	7.4 ± 1.8	7.3 ± 1.7	7.9 ± 1.2	6.3 ± 0.6	6.9 ± 0.9
+P	11.2 ± 2.6	11.2 ± 0.5	10.3 ± 0.5	9.5 ± 1.18	10 ± 0.6	6.6 ± 0.7	6.7 ± 0.6	11.3 ± 0.7	8.4 ± 0.6	8 ± 1.8	7.4 ± 0.7
+N	13.8 ± 1.6	16.7 ± 1.0	15.7 ± 0.8	8.6 ± 0.4	11 ± 1.3	8.9 ± 0.8	10.3 ± 0.7	10.7 ± 1.4	9.6 ± 0.7	8.9 ± 1.5	7.2 ± 0.4
+NP	14.4 ± 1.7	17.2 ± 0.9	16.5 ± 1.5	12.6 ± 0.5	15.3 ± 3.7	10.3 ± 2.4	10.9 ± 1.5	15.2 ± 2.9	11.8 ± 1.7	11.1 ± 1.3	9.8 ± 1.4
Interaction (%)[a]	56	11	10	119	36	−5	59	7	77	12	283

Values are given in t DMY ha^{-1} together with standard deviation ($n = 4$) measured on the Angladure long-term field experiment (Ercé, French Pyrenees) from 1999 to 2009

[a] Interaction (%) = 100 × [(yield response to N and P) − (yield response to N + yield response to P)]/(yield response to N + yield response to P)

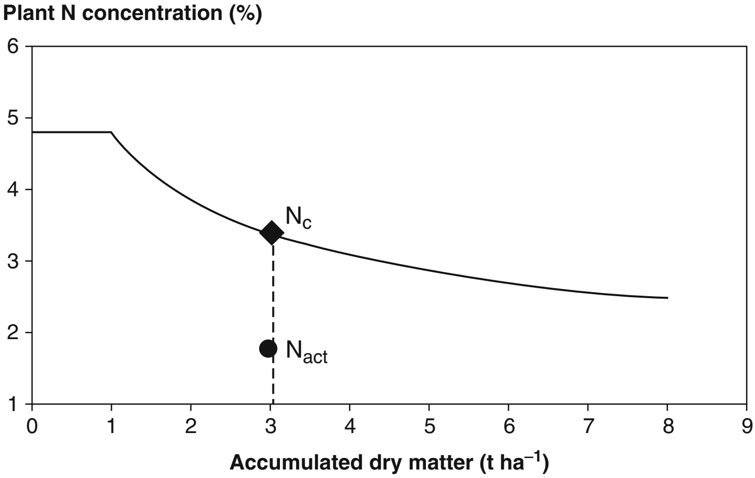

Fig. 11.2 Determination of the nitrogen nutrition index (Ni); Ni = N_{act}/N_c where N_{act} is the measured concentration and N_c is the optimum value obtained from the critical N curve (adapted from Lemaire and Gastal 1997)

concentration during sward growth is dependent on the N application rate. Consequently, they proposed the following relationship: $P\%_{\text{critical}} = 0.15 + 0.065\ N\ \%_{\text{measured}}$, which provides, at a given time, the minimal P concentration in a sward needed to produce maximum dry matter. This relationship remains linear within the range of N and P concentrations observed in grasslands. Similarly to Ni, they proposed calculation of a P nutrition index (Pi) as the ratio of $P\%_{\text{measured}}$ in the given sward to $P\%_{\text{critical}}$ obtained with the critical P curve, expressed as a percentage. Whichever nutrient is considered (N or P), the nutrition index indicates the extent to which the sward nutrient requirements for maximum growth have been fulfilled by the fertilizer inputs and/or the soil nutrient reserves. In practice, indices vary between values above 100 (signifying an adequate or excessive nutrition level) to below 40 (indicating severe deficiency). Duru and Ducrocq (1997) applied this method to diagnose both a set of natural swards with severe P deficiency and a legume fraction contributing to less than 20% of the total harvested biomass. They showed that this index gives an accurate diagnosis of the P nutrition level during growth, albeit after the event. More recently, the approach has been extended to corn (Ziadi et al. 2007) and spring wheat (Ziadi et al. 2008). In practice, index values are used in France by the extension services to make fertilizer recommendations for farmers (Thélier-Huché et al. 1999). This approach appears to be more reliable than those based either on a single critical concentration (Pinkerton and Randall 1994) or a nutrient concentration ratio (Walworth et al. 1986; Bailey et al. 2000). In the field of ecology, N:P ratios are used in order to determine whether biomass production is N- or P-limited at community level. The review by Güsewell (2004) reports that terrestrial plant communities with N:P < 10 are N-limited and those with N:P > 20 are P-limited; as a consequence biomass production should be enhanced by N or P fertilization, respectively.

11.2.2.2 Relationships Between Nutrition Indices and Growth: Analysis of N–P Interaction

The nutrient index approach has been used by agronomists to establish relationships between N nutrient status of swards and biomass production. Lemaire and Gastal (1997), for sown grasslands, and Duru and Ducrocq (1997) for permanent grasslands demonstrated that with non-limiting P and water supply there is a direct relationship between Ni and the relative yield, i.e. the ratio of DMY measured to maximum DMY, expressed as a percentage. From this, the Ni was used to quantify the DMY response of grassland swards to N and P supply (Duru and Ducrocq 1997) and their interactions, and to analyse more precisely the interactions between mineral nutrition and water supply (Duru et al. 2000; Gonzales-Dugo et al. 2005; Mills et al. 2009). As an example, we show in Fig. 11.3 the relationship between Ni and the relative response to N and P for the Angladure grassland established for the first growth cycle in 2007. For this first harvest, the biomass production measured represents 39%, 47%, 38% and 40% of the total annual biomass production (Table 11.1) for control, +P, +N and +NP treatments (N0P0, N0P1, N1P0 and N1P1 in Fig. 11.3), respectively. The relative response was calculated as the ratio of

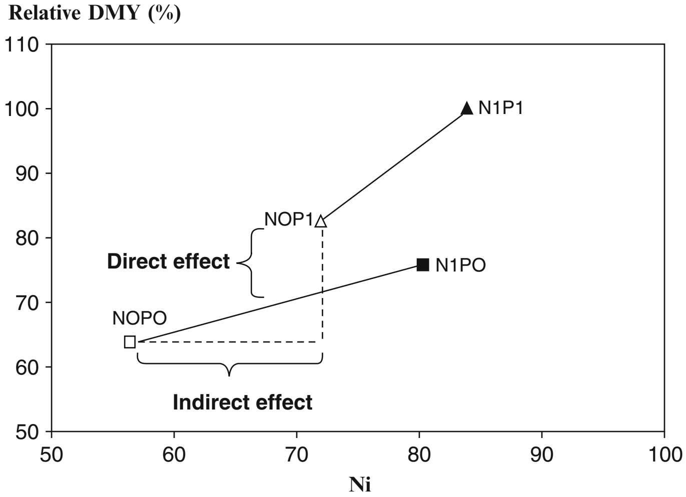

Fig. 11.3 Relationship between the relative response ($DMY_{treatment}/DMY_{optimum}$) and N nutrition index (Ni) for the first growth cycle measured in 2007 on the Angladure experiment grassland (Ercé, French Pyrenees). The direct effect on growth represents the increase of the sward efficiency for N conversion in biomass for +P treatments; the indirect effect on growth is a consequence of the increase in N nutrition status of the sward for +P treatments. *N0P0* control, *N1P0* + N treatment, *N0P1* + P treatment, *N1P1* + NP treatment

the DMY measured on a given treatment to the maximum DMY (on N1P1 plots). From Fig. 11.3, it is possible to identify graphically the response in terms of nutrient status. Comparison of the N0P1 treatment with the control (N0P0) quantifies the increase in growth in response to P supply, which results from the indirect effect of P and increases the N nutrition status (Ni passes from 55 to 72), and the direct effect of P on growth, which increases the sward efficiency for N conversion in biomass. The sward is more efficient in converting N into biomass under non-limiting P supply than with limiting P supply; the slope for the P1 treatments (upper line in Fig. 11.3) being higher than the slope for the P0 treatments (lower line in Fig. 11.3) (Duru and Ducrocq 1997).

Several hypotheses are proposed to explain the increase in N nutrition level of the sward following P supply (indirect effect). The first is that improved P nutrition status increases the growth of aerial parts and the root system and thus improves soil exploration capacity by the root system and, hence, nutrient interception (Duru 1992). This process is particularly efficient in the drainage phase when improved root colonization of the soil can lead to better interception of mobile nutrients such as nitrate-N. As an example, the spectacular interaction observed in 2002 (Table 11.1) can be explained by these processes; heavy rainfall in spring led to a positive water balance, the amount of drained water being much more significant than usual, i.e. 900 mm instead of 400 mm on average. As a consequence, N losses were greater in N1P0 than in N1P1 plots, where adequate plant P nutrition allowed better root growth and, consequently, better interception of nitrate in the soils. Another hypothesis concerns the effect of P on organic matter mineralization: increased P supply leads to increased soil N internal recycling (mineralization and nitrification) because of a P-limited soil biomass and/or improved litter quality (Parfitt et al. 2005). The effect of P fertilization on legumes is presented in Sect. 11.3.2.

11.3 Indirect N–P Interactions

11.3.1 Indirect Interactions Related to Grassland Vegetation Types

11.3.1.1 Definition of Plant Functional Types and Grassland Vegetation Types from Plant Functional Traits

In the field of plant ecology, the development of a functional approach has provided new methods based on an analysis of the functional traits developed by plants growing in communities. The determination of the functional composition of the vegetation can be based on the identification of a PFT, which defines a group of species that fulfil similar functions in the ecosystem, without necessarily presenting phylogenetic relationships (Gitay and Noble 1997). In order to better understand ecosystem behaviour, one needs to define the functional groups associated with the main processes taking place in the ecosystem, and the species most characteristic of these groups (Hooper and Vitousek 1997). These species correspond to the dominant ones present in the community because they represent the largest pool of matter and energy, and control its structure and behaviour (Goldberg 1997). A group brings together species that share common values of one or several functional traits, i.e. biological characteristics (morphological, physiological, phenological, demographic etc.) that are the expression of similar behaviour or strategies. One distinguishes response traits, whose values change in response to environmental factors or agricultural practices (fertilization and/or defoliation regime), and effect traits, which act on the processes of the ecosystem (productivity and nutrient cycling among others) (Lavorel and Garnier 2002). This functional approach has been used by Ansquer et al. (2004) to identify different PFTs based on the measurement of the leaf dry matter content (LDMC) for grasses in a community (Table 11.2). These plant types have been used to develop a simplified method to determine the functional composition of the grassland vegetation at the community scale, and to define grassland vegetation types (GVTs). In their recent work, Ansquer et al. (2009a, c) demonstrated that the identification of PFTs is an operational approach for assessing agricultural services defined in terms of productivity, phenology and quality.

11.3.1.2 Relationships Between Response Traits and Fertility Gradients

The value of traits varies in response to both nutrient availability and defoliation regime. Thus it becomes possible to group species according to the strategies they employ to adapt to different habitats; grassland species can be ranked according to their aptitude for acquisition, or conservation of nutrients and carbon. For instance, species adapted to nutrient-rich environments, such as *Lolium perenne*, will display resource capture strategies. The corresponding foliar traits are a high specific leaf area (SLA) and low LDMC. Conversely, species adapted to low fertility environments that display nutrient conservation strategies, such as *Briza media* and *Festuca ovina,* have low SLA and high LDMC values. Besides these traits, which are relatively easy to measure, others should be considered, either because their

Table 11.2 Plant functional types (PFTs) of grass species defined on the basis of a hierarchical analysis applied to dry matter contents of leaf blades (LDMC) (Ansquer et al. 2004)

Type A	Type B	Type C	Type D
Holcus lanatus, *Lolium perenne*	*Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Festuca arundinacea*, *Poa trivialis*	*Agrostis capillaris*, *Avena pubescens*, *Festuca rubra*, *Phleum pratense*, *Trisetum flavescens*	*Brachypodium pinnatum*, *Briza media*, *Cynosurus cristatus*, *Deschampsia caespitosa*, *Festuca ovina*

agronomic impact is important or because they better account for the species' capacity to succeed in the competition for nutrients.

For instance, species that display resource conservation strategies have a leaf lifespan (LLS) longer than that of species with acquisition strategies, and consequently are more efficient in the use of mineral resources. This is evaluated by measuring their nutrient use efficiency (NUE), i.e. the crop yield per unit of nutrient absorbed (Ryser 1996). This efficiency results from two components: (1) the productivity associated with a given nutrient (the amount needed for one unit of biomass production) and (2) its mean residence time (MRT) in leaves (Berendse and Aerts 1987).

As a case study for P and N NUE, Table 11.3 shows an experiment conducted on *Dactylis glomerata* and *Festuca rubra* transplanted into grassland that initially displayed low N and P fertility levels. In order to differentiate N and P nutrition levels, three treatments were applied: +N, +P and +NP. N and P were applied at 0 and 150 kg ha^{-1} as NH_4NO_3 and triple superphosphate. N and P supply provided non-limiting nutrition conditions, whereas the unfertilized control displayed N- and/or P-limiting nutritional status.

Under N-limited growth conditions, DMY was increased by 33% by P, but this increase was not significant. Under non-limiting N growth conditions, there is a significant increase in DMY following P supply. Under both N levels, there was no difference in DMY between the two species.

Under N-limiting growth conditions there is a significant effect of the species on the NUE for N, which increases in response to P limitation: by 4 points (from 51 to 55) for type B species (*Dactylis glomerata*) and 7 points (from 60 to 67) for type C (*Festuca rubra*). Under non-limiting P supply, NUE for P is significantly different between species, NUE for *Festuca rubra* being 25% higher than for *Dactylis*. For both species, increasing P stress on control plots leads to an increase in NUE for P, but the values for the two species are not significantly different. Under non-limiting N supply, we do not observe any significant change in NUE for N and P in response to P stress. It is likely that when N nutrition is non-limiting, both species are better able to adapt to P stress than when N is limiting. This experiment demonstrates that both species increase their NUE for N and for P when their availability decreases, as expected (Lajtha and Harrison 1995). However, the size of the response varies according to the species, type C (*Festuca rubra*) always displaying higher NUE than type B (*Dactylis glomerata*) for the same amount of forage production. As an example, a *Dactylis glomerata* sward would export more P and more N than a *Festuca rubra* one (25% and 15% more on average in our case). We need to keep in mind that some treatments forced both species to grow under fertility levels different from those usually met, i.e. limiting N and P for *Dactylis* and ample N and P supply for *Festuca*. The NUE values measured in their natural habitats would be different, close to that of the N- and P-limiting treatment for *Festuca* and N and P non-limiting treatment for *Dactylis*. In natural habitats, *Festuca* is most likely to display high NUE values (67 and 757 for N and P, respectively) and *Dactylis* low values (36 and 233 for N and P, respectively).

Table 11.3 Comparison of *Dactylis glomerata* and *Festuca rubra* responses to P, N and NP

	N − P−			N − P+			N + P−			N + P+		
	NUE_N (kg DM kg^{-1} N)	NUE_P (kg DM kg^{-1} P)	DMY (t ha^{-1})	NUE_N (kg DM kg^{-1} N)	NUE_P (kg DM kg^{-1} P)	DMY (t ha^{-1})	NUE_N (kg DM kg^{-1} N)	NUE_P (kg DM kg^{-1} P)	DMY (t ha^{-1})	NUE_N (kg DM kg^{-1} N)	NUE_P (kg DM kg^{-1} P)	DMY (t ha^{-1})
Dactylis glomerata	55^a	717	2.4	51^a	375^a	3.2	26	496	2.8	36	233	4.5
Festuca rubra	67^b	757	2.4	60^b	459^b	3.2	28	510	2.9	28	209	4.5

DMY average dry matter yield, NUE_N nutrient use efficiency for N, NUE_P nutrient use efficiency for P. All measurements were made at the first cut ($n = 3$)
Figures in a column followed by different letters are significantly different ($P < 0.001$)

11.3.1.3 Relationships Between Plant Functional Types and Nutrient Cycling

In order to illustrate the relationships existing between PFT and nutrient cycling, we rely on a survey conducted in 2001 on a garden collection of 16 grasses representing the four types described in Sect. 11.3.1. The grasses were grown in Auzeville (France) with non-limiting mineral and water supply. The nutrient concentrations were measured for the spring growth cycle on the youngest adult leaves, and then for senescent leaves in July. Under similar growing conditions, P concentrations for green tissues vary between 0.21% and 0.41% according to species and type; meanwhile N concentrations vary between 2.1% and 3.8%. Species with conservation strategies (types C and D) tend to have lower N and P concentrations than species with acquisition strategies (types A and B). In parallel, large variations in N and P concentrations are observed for the senescent leaves. When we plot the N:P ratios of the green tissue as a function of N:P ratios for senescent ones (Fig. 11.4), we observe an increase in N:P ratio from type A to type D, varying from 6.6 to 14.8. We also note that for all species, N:P ratios are lower for senescent leaves than for green ones; they vary between 2.7 and 9.7, indicating that for all these species and under these growing conditions, resorption efficiency is higher for N than for P.

These examples demonstrate that differences in species strategies for resource acquisition lead to wide ranges in mineral concentrations for residues and litter returned to the soil, with positive or negative feedback on the rate of P cycling: according to N:P and or C:P ratios, either mineralization or immobilization pathways will control P cycling and its availability for plants (White and Tayoub 1983; Güsewell et al. 2005). Similarly, comparing ten contrasting sites in Europe, Fortunel et al. (2009) demonstrated that species with conservation strategies have a

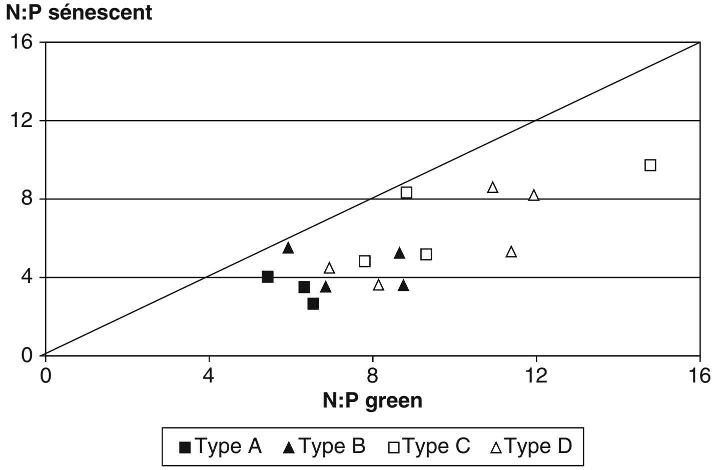

Fig. 11.4 Relationship between N:P ratio measured on green leaves and senescent leaves for 16 grasses representative of the four plant functional types defined by Ansquer et al. (2004) (see Table 11.2 for examples)

chemical composition that results in slower decomposition rates of litter and residues, lengthening the time until nutrients will again become available for plants.

11.3.2 Effects of P on Biological Nitrogen Fixation

There is a general consensus that N application will often favour grasses, which are more competitive than legumes under non-limiting N, and thus result in a decline in the proportion of legumes in grassland communities (Laidlaw and Withers 1998; Loiseau et al. 2001). In contrast, for low residual heights, a frequent cutting regime and absence of N fertilization are practices frequently reported to maintain or increase clover content in mixed swards (Barthram et al. 1992). Conversely, P fertilization alone**,** associated with intense defoliation, will often favour the development of legumes. These trends are acknowledged for grazed grasslands and rangelands (Aydin and Uzun 2005; Martiniello and Berardo 2007) as well as grasslands cut for hay (Nevens and Rehuel 2003; Jouany et al. 2004). This increased contribution of legumes to the sward biomass in response to P fertilization leads to an increase in the sward N concentration because the N concentration of the legume fraction is generally higher than that of the grass fraction (Mackay et al. 1995; Henkin et al. 1996). As a consequence, the N:P ratio for pure legume swards or associations remains generally higher than that of grass swards (Jouany et al. 2004). Results in the literature show that when P is limiting, nodule growth and N_2-fixation activity are limited (Haynes and Ludecke 1981). Høgh-Jensen et al. (2002) demonstrated that under low P availability, white clover displays whole-plant adaptative responses by modifying the relative growth of shoots, roots and nodules. From an agronomic point of view, one should keep in mind that optimization of P nutrition might help in maximizing N inputs into grasslands by symbiotic N fixation.

11.4 Analyzing the Effect of Herbivores on N and P Cycles in Grassland Ecosystems

Most of the grasslands in the world are grazed by large herbivores, mostly domestic herds of ruminants grazing at low intensity (Allard et al. 2003). This being so, the biogeochemistry of major elements (e.g. N or P) in grasslands cannot be thoroughly addressed without considering the role of grazers. The effect of grazing on the N and P cycles has been highlighted by numerous empirical and experimental studies (Hobbs 1996). In short, terrestrial grazers have been shown to promote soil nutrient heterogeneity through the concentration of faeces and urine in specific parts of the landscape (Augustine 2003; Augustine and Frank 2001), to increase soil nutrient availability through faeces and urine deposition (Carline et al. 2005), to decrease soil nutrient availability through the selective grazing of plants producing good nutrient recycling litter (Pastor et al. 1993), and to affect the coupling between the N and P cycles (Frank 2008), with important consequences for the intensity of, and limitations on, primary production.

The combined direct (grass consumption) and indirect (recycling through urine and/or faeces deposition) effects of herbivores have been studied using various experimental setups. For instance, controlled grazing in enclosures (Allard et al. 2003) versus deposition of faeces in exclosures to prevent grazing can, hence, disentangle the direct and indirect effects of the herbivores (Van der Wal et al. 2004). Artificial clipping and deposition of synthetic urine in mesocosms (Attard et al. 2008) have been performed. From these studies, it appears that the net effect of grazers on nutrient cycles and its consequences for primary production seem not to follow a general rule. Instead, they appear to vary across locations and to be dependent on other factors, such as the climate, the nature of the bedrock etc. (Augustine and McNaughton 2006; Frank and Groffman 1998; Frank 2008; Van der Wal et al. 2004). Yet the effect of grazers is generally significant and, in some cases, the combined effect of grazing and other factors (e.g. the increase in atmospheric N deposition) on biogeochemical cycles can even lead to serious habitat degradation (Van der Wal et al. 2003). For some specific cases, the mechanistic interpretation of the herbivore effect on nutrient cycles is trivial. For instance, by preferentially consuming legumes herbivores can decrease N fixation and, hence, decrease the soil N budget (Ritchie et al. 1998). Yet, in most cases the mechanisms are less obvious, and most authors mention the complexity of the soil processes and stress the indirect effect of grazers on the community structure of soil microorganisms (Carline et al. 2005). For instance, artificial defoliation in grassland has been shown to reduce root biomass and affect the structure of soil food webs, with consequences for the soil inorganic N budget (Mikola et al. 2001). Other experiments have concluded that a decrease of soil microbial respiration follows artificial defoliation, probably due to the fact that defoliation reduces the labile carbon available to soil microbes (Stark and Kytöviita 2006). On the other hand, urine deposition has been shown to affect the community structure of soil bacteria, especially ammonia-oxidizing and nitrite-reducing bacterial communities, which in turn affect the N cycle and budget (Orwin et al. 2010). Again, the magnitude of these effects is greatly variable and seems to depend on other factors such as soil moisture, trampling etc. (Sørensen et al. 2009).

On the other hand, modelling approaches have stressed the effect of grazers on the speed of recycling and on nutrient budgets in the soil–vegetation compartment (e.g., De Mazancourt et al. 1998, 1999). This kind of insight can help a lot with the interpretation of data. However these modelling approaches have focussed on the cycling of only one nutrient and, to our knowledge, the case of coupled cycles of two or more nutrients has not been thoroughly addressed. Some insights could come from limnology, where the effect of planktonic grazers on the coupling between the cycles of N and P has long been studied (Frank 2008). In pelagic aquatic ecosystems, planktonic biomass represents the main stock of nutrients and planktonic grazers can represent a significant fraction of this stock (Andersen 1997). In this context, models have shown that the ratio of nutrients in planktonic grazers can affect the ratios of nutrients available to algae, with important consequences for algal community structure and nutrient limitation status (Sterner 1990; Andersen 1997; Daufresne and Loreau 2001). These results suggest that one cannot understand the effect of grazers on the P cycle without considering the N cycle. Yet, these results are not readily applicable to terrestrial ecosystems, where the nutrient fraction stored in the herbivore biomass is usually negligible compared to that stored in the soil–vegetation system. Hence, the study of grassland ecosystems requires the derivation of specific soil–grass–grazer models incorporating both the N and P cycles. Because the soil N and P represent the main stocks of nutrients in grassland, it is expected that the effect of the grazers on the loss rates of N and P from the soil will have a key effect on the N:P ratio in these systems. In particular, the higher sensitivity of N to leaching and to volatilization (Ambus et al. 2007), in comparison to P, should play an essential role. These models should provide valuable theoretical tools for predicting the effect of grazing on the N and P cycles in grassland, and should shed some light on the interpretation of empirical patterns.

11.5 Conclusion

The approaches and case studies introduced in this chapter highlight the importance of studying biological P cycling in relation to that of N. A comprehensive approach to nutrient cycling in grassland ecosystems, whether cultivated or natural, needs to be considered when developing sustainable production systems with environmental and economic constraints. Experimental approaches developed in recent years by agronomists and ecologists have led to a better understanding of the interactions between N and P and their effects on ecosystems. Long-term field experiments are essential for analysis and evaluation of these interactions. There still remain some aspects that deserve more attention in the future:

1. Although studies conducted on a field scale have demonstrated that there is similarity between grasses and dicots for plant phenology (Ansquer et al. 2009b) and that grasses and dicotyledonous (especially rosette) plant life forms behave very similarly (Ansquer et al. 2009a), little is known about similarities and differences in nutrient use and recycling processes between different life forms. This point is important when considering the role of legumes in N–P interactions in grassland.
2. We now need to improve our knowledge of the effects of global climate change on P biological cycling. Direct effects as a consequence of decreased water availability or indirect ones as a consequence of dramatic changes in vegetation can be expected from global warming.
3. The derivation of specific soil–grass–grazer models incorporating both the N and P cycles should provide valuable theoretical tools to predict the effect of grazing on the N and P cycles.

4. Finally, one aspect of the question remains unexplored, it concerns the soil microbial community and its function in regulating nutrient fluxes. Improved knowledge of the interactions between soil biota and plants and grazing animals should help in developing more efficient and sustainable grassland systems.

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