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Former land use affects the nitrogen and phosphorus concentrations and biomass of forest herbs

BAETEN Lander^{1,*}, VERSTRAETEN Gorik¹, DE FRENNE Pieter¹, VANHELLEMONT Margot¹, WUYTS Karen¹, HERMY, Martin² and VERHEYEN, Kris¹

¹ *Laboratory of Forestry, Dpt. Forest and Water Management, Ghent University, Geraardsbergsesteenweg 267, B-9090 Gontrode (Melle), Belgium*

² *Division of Forest, Nature and Landscape, Dpt. Earth and Environmental Sciences, K.U.Leuven, Celestijnenlaan 200E, B-3001 Leuven, Belgium*

* Corresponding author: Lander.Baeten@UGent.be, Fax: ++32 (9) 264 90 92

Abstract

The colonization rates of understorey plants into forests growing on former agricultural land differ remarkably among species. Different dispersal and recruitment largely account for the contrasting colonization rates, but different effects of the soil legacies of former agricultural land use on plant performance may also play a role. Seven herbaceous forest species were sampled in paired post-agricultural and ancient forest stands to study whether land-use history has an effect on the aboveground nutrient concentrations (N, P and N:P ratios) and biomass of forest herbs and, if so, whether slow and fast colonizing species respond differently. Results showed that P concentrations were significantly affected by former land use with higher concentrations in the post-agricultural stands. N concentrations were unaffected and N:P ratios were significantly higher in the ancient stands. Nutrient concentrations varied considerably among species, but the variation was unrelated to their colonization capacity. Six out of the seven species had higher biomass in the post-agricultural stands relative to the ancient stands, and the degree to which the species increased biomass was positively related to their colonization capacity, i.e., the fast colonizing species showed the strongest increase. Such differential responses to past land use may contribute to the contrasting colonization capacity of forest plants. Land-use history thus affected both the nutrient concentrations and biomass of forest herbs, and only the biomass response was related to colonization capacity.

Key-words: secondary succession, post-agricultural forest, colonization; introduction experiment, plant performance, phosphorus, N:P ratio

Introduction

The availability of nitrogen (N) and phosphorus (P) to terrestrial vegetation profoundly influences several aspects of community dynamics such as plant performance, plant species interactions and multitrophic interactions (e.g., Aerts and Chapin 2000; Güsewell 2004; Craine 2009). Consequently, environmental changes that alter the levels of N and P supply may have a significant impact on the structure and composition of plant communities. Determining the response of plants to those novel environmental conditions is therefore one of the challenges of applied ecological research.

For forest understorey communities, land-use change forms among the most radical and large-scale environmental changes in much of Europe and eastern North-America. In many landscapes, large parts of the present-day forest area have not been continuously forested during the past decades or centuries, but were in fact established on former agricultural land in a recent or distant past ('post-agricultural' forest) (reviews: Flinn and Vellend 2005; Hermy and Verheyen 2007). Previous studies found that the performance of forest plants may considerably differ between post-agricultural forests and forests without historical records of past agricultural use ('ancient' forest) (Endels et al. 2004; Verheyen and Hermy 2004; Vellend 2005; Fraterrigo et al. 2006; Baeten et al. 2009a). Those performance differences, which can be either enhanced or depressed in post-agricultural forest, may be related to the soil nutrient legacies of the historical land use. The past agriculture may have a persistent impact on the present-day soil N and P state: the soil P is generally higher in previously fertilized forest compared to ancient forest and the soil N may be lower, equal or higher (e.g., Koerner et al. 1997; Verheyen et al. 1999; De Keersmaecker et al. 2004; Falkengren-Grerup et al. 2006; Dambrine et al. 2007). While pot experiments have demonstrated that some forest plants may increase their performance in response to increased N and P availability (Pigott and Taylor 1964; Elemans 2004; Hips et al. 2005; Baeten et al. 2010), the results still need to be extended to field conditions (but see Falkengren-Grerup et al. 2006; Fraterrigo et al. 2009).

Forest plant species differ considerably in their capacity to colonize post-agricultural forests. Some species already appear soon after canopy closure, but for others it may take several decades to centuries. Dispersal constraints initially cause the limited colonization abilities (reviews: Verheyen et al. 2003b; Vellend et al. 2007), but the effects of past land use on plant performance may also play a role (Vellend 2005; Baeten et al. 2009a). Within the perspective of the potentially altered N and P supply in post-agricultural forests, we questioned whether differences in the colonization capacity among forest plants were associated with variation in their plasticity in response to N and P. If fast colonizing species also tend to increase their performance more at increased nutrient levels compared to slow colonizers this would imply that the community recovery in post-agricultural forests is not only controlled by dispersal, but also by the soil nutrient legacies of past land use.

Here we determined the effect of former agricultural land use on the aboveground nutrient concentrations (N, P and N:P ratios) and total biomass (as a measure of performance) of seven common forest herbs in valley forest stands in northern Belgium. We used two experiments in which a set of slowly colonizing forest herbs were introduced into post-agricultural forest ten and eight years ago (Baeten et al. 2009a, b). In this way, we could sample both slowly colonizing species (introduced) and fast colonizing species (resident community). We hypothesised that (1) land-use history has a significant effect on the nutrient concentrations and biomass of the forest herbs; (2)

there is considerable variation among species and (3) the interspecific variation is related to the colonization capacity of species with the fast colonizing species showing the most plastic response.

Methods

Study sites and soil samples

Plant tissue of seven forest herbs was collected in post-agricultural and continuously forested ancient forest stands (*sensu* Hermy et al. 1999) at three different forest sites in northern Belgium: two separate introduction experiments and one additional site with spontaneous colonization. All sites were on moist, eolian, loamy soils that supported a mesotrophic vegetation characteristic of valley forest. The main canopy species were *Populus* \times *canadensis*, *Fraxinus excelsior* and *Corylus avellana*. Regional average (1971–2000) annual temperature is 10.1 °C and the average annual precipitation amounts to 820 mm (Royal Meteorological Institute, www.kmi.be).

The first introduction experiment was set up in the forest ‘Muizenbos’ in 1999 (51.197 °N, 4.566 °E). Experimental populations of *Primula elatior*, *Anemone nemorosa*, *Ranunculus ficaria* and *Geum urbanum* were established in two ancient stands (forest for more than 145 year based on land-use maps) and four post-agricultural stands (c. 15 year old) on former heavily fertilized grassland. In each stand, every species was introduced by sowing seeds in six 0.5 m \times 0.5 m plots or planting adults or ramets (for geophytes) in six similar plots. The twelve plots were regularly distributed in a 12 m \times 12 m fenced area. For the present study, we sampled the two ancient stands and two of the post-agricultural stands. More details on the design of the experiment and population dynamics are reported in Verheyen and Hermy (2004) and Baeten et al. (2009a).

The second introduction experiment was initiated in a forested landscape 20 km east of Brussels in 2002 (‘Doode bemde’ nature reserve; 50.827 °N, 4.642 °E). Six forest herbs, including *P. elatior*, *A. nemorosa* and *G. urbanum*, were introduced in two valley forest stands that were established on former agricultural land between 1909 and 1940. In each stand, the species were sown into twelve 0.5 m \times 0.5 m plots that were also regularly distributed in a 12 m \times 12 m fenced area. For the present study, we only sampled plants from one of the stands because the canopy of the other stand was dominated by *Alnus glutinosa* (a N-fixing species), which could alter the soil N concentrations. Because the species were only introduced into post-agricultural forest, we also sampled plant material in a 12 m \times 12 m area in a nearby ancient stand (420 m away). The ancient stand had been forest for more than 224 years (based on Verheyen et al. 2003a) and was characterized by a similar soil and canopy. Baeten et al. (2009b) give more details on the design of this introduction experiment.

Finally, we also sampled plants in a post-agricultural and adjacent ancient stand of a third forest site ‘Aelmoeseneiebos’ (50.975 °N, 3.795 °E). Unlike the other two sites, the slowly colonizing forest species had not been introduced here but they had colonized spontaneously. Colonization probably occurred from the source populations in three adjacent ancient forest stands. The post-agricultural stand was established in 1968 on former grassland, while the ancient stand had been forested at least since 1775. At this forest site, we also sampled plant tissue in 12 m \times 12 m areas.

At each forest stand, we took five soil samples (0–10 cm depth) and merged them into a single mixed soil sample. The mixed samples were dried for c. 48 h at 40 °C and analysed for pH-KCl, total P (nitric-

perchloric acid digestion) and ammonium acetate-EDTA extractable P (as an indicator for plant available P). The P concentrations were measured colorimetrically by the molybdate method of Scheel (1936). Total N and C were measured by dry combustion at 850 °C using an elemental analyzer Vario MAX CNS, Elementar.

Study species, sampling and chemical analyses

Seven common forest herbs that naturally occur in mesotrophic valley forest and represent a range of colonization abilities were sampled (Table 1). In addition to the species that were introduced in the experiments (*A. nemorosa*, *P. elatior*, *G. urbanum* and *R. ficaria*), we also sampled plant material from spontaneous populations of three other forest herbs with moderate (*Circaea lutetiana*) and high (*Aegopodium podagraria*, *Urtica dioica*) colonization abilities. In this way, we could determine whether fast colonizing forest herbs may respond differently to the former land use in terms of N and P uptake and biomass production compared to slow colonizers. The colonization capacities of the forest species were based on a review study by Verheyen et al. (2003b), in which a species-specific colonization capacity index (CCI) was calculated based on the species' affinity to ancient forest across 12 studies in north-western Europe. The CCI ranges between -100 (fast colonizer) and +100 (slow colonizer).

Table 1 Life form, phenology and colonization capacity of the sampled forest herbs. The CCI is the colonization capacity index from Verheyen et al. (2003b) and ranges from 100 (slow colonization into post-agricultural forest) to -100 (fast colonization).

Species	Family	Life form	Leaf phenology	CCI
<i>Anemone nemorosa</i>	Ranunculaceae	Geophyte	Vernal	77
<i>Primula elatior</i>	Primulaceae	Hemicryptophyte	Vernal-aestival	67
<i>Circaea lutetiana</i>	Onagraceae	Geophyte	Aestival	67
<i>Ranunculus ficaria</i>	Ranunculaceae	Geophyte	Vernal	11
<i>Geum urbanum</i>	Rosaceae	Hemicryptophyte	Winter green	-33
<i>Aegopodium podagraria</i>	Apiaceae	Hemicryptophyte	Aestival	-45
<i>Urtica dioica</i>	Urticaceae	Geophyte/ Hemicryptophyte	Aestival	-71

In each forest stand, we collected the total aboveground biomass for a maximum of five random individuals of each species (three or four individuals in a few cases). For the geophytes, we sampled a number of ramets in five separate patches (to obtain enough biomass for analysis). The average number of ramets (\pm SE) collected per patch was 13.9 ± 3.4 for *A. nemorosa*, 5.4 ± 1.3 for *C. lutetiana* and 8.5 ± 3.0 for *R. ficaria*. Sampling occurred following peak flowering, i.e., in the first week of May for the three vernal species and in the first week of July for the other species. Next, the collected individuals or ramets were dried to constant weight for c. 48 h at 70 °C. The biomass of each sample

was weighted (± 1 mg), and for the geophyte samples, the average ramet biomass was calculated (total mass/number of ramets). Plant material was analysed for total N concentrations (mg N/100 g dry biomass) with the Kjeldahl method. Total P concentrations (mg P/100 g dry biomass) were measured colorimetrically by the molybdate method (Scheel 1936) following a di-acid digestion (HNO₃ 65%, HClO₄ 70%, 5:1).

Data analysis

We applied linear mixed models to account for the variation in N and P concentrations and N:P ratios among (1) the forest sites, (2) the forest stands nested within sites and (3) the different species. The models tested the effect of three explanatory variables: the land-use history of the stands (post-agricultural versus ancient), the colonization capacity of the species (CCI index) and the biomass of the sampled individuals as a co-variable. Following Zuur et al. (2009), we first selected the optimal random effects structure based on a likelihood ratio test between models with the same fixed component (the three explanatory variables), but a different random component. The optimal model included 'Forest stand' and 'Species' as non-nested random effects, i.e., the variation among forest sites was not substantial. Next, we compared the model that included the three explanatory variables with a model that dropped one of those variables to test the significance of that particular variable (χ^2 test statistic, likelihood ratio test; Zuur et al. 2009). Finally, we also calculated the proportion of the total variation in the response variable that was associated with variation among different forest stands and among different species ('intraclass correlations') and the amount of this variation that was explained by the explanatory variables. All calculations were performed using the lmer function in the lme4 package in R version 2.9.1 (R Development Core Team 2009; Bates & Maechler 2010).

The effect of 'Land use' (post-agricultural versus ancient) on the total aboveground biomass was tested in a similar way, but for each species separately because of their inherent differences in biomass related to growth form. The optimal random effects structure only included 'Forest stand', i.e., 'Forest site' did not account for additional variation. The significance of 'Land use' was also tested by comparing the mixed models with and without the factor based on a likelihood ratio test. Finally, we calculated the ratio between the average biomass of a species in the post-agricultural versus the ancient stand for each forest site. The average ratio for each species across the three sites was related to its colonization capacity index by means of linear regression.

Results

Values for soil pH-KCl, total N and C were comparable between ancient and post-agricultural stands (Table 2). The average C:N ratio was 12.6 (± 0.2) in ancient and 11.5 (± 0.3) in post-agricultural stands. Land-use history did have an effect on the total and plant available soil P concentrations with higher levels in the post-agricultural stands. The total N concentration in the aboveground biomass of the seven forest herbs was unrelated to the former land use, the colonization capacity and the biomass of the sampled plants (Table 3; Fig. 1a). The total plant P concentrations did differ between stands with different land-use histories. In post-agricultural forest stands, P concentrations were consistently higher in all species compared to ancient stands (Fig. 1b). Almost half of the variation in P concentrations (46.3 %) was associated with variation between stands, and land-use history explained 66.5 % of this variation. There was also considerable variation among species – 18.8 % of the variation in P concentration was attributable to species-specific differences – but this variation was unrelated to the colonization capacity of the species. The patterns for the N:P ratios were similar. Land-use history had a significant impact on the N:P ratios, which were consistently lower in post-agricultural versus ancient stands (Table 3; Fig. 1c). A large proportion of the total variation in N:P ratios was associated with variation between stands (59.4 %), and land use accounted for 69.1 % of this variation. Species-level variation was 15.5 %, but was unrelated to the colonization capacity of the species.

Table 2 Chemical soil properties (0–10 cm) of the ancient (A) and post-agricultural stands (P-A) at the three forest sites where the forest herbs were sampled. We used an ammonium acetate-EDTA extraction of soil P as an indicator of plant available P (P-plant) and an extraction of the total P fraction (P-total).

	Muizenbos				Doode bemde		Aelmoeseneiebos	
	A	A	P-A	P-A	A	P-A	A	P-A
pH	6.4	4.7	4.5	4.2	6.0	5.4	4.5	5.5
P-total (mg/100g)	37.1	28.2	107.5	75.4	65.4	104.5	37.1	57.0
P-plant (mg/100g)	0.70	0.68	7.81	6.24	2.37	2.19	1.20	4.74
N (g/100 g)	0.25	0.19	0.24	0.21	0.31	0.36	0.37	0.22
C (g/100 g)	3.11	2.44	2.79	2.53	3.74	3.82	4.76	2.54

Table 3 Effects of Land use, Colonization capacity and Biomass on the N and P concentration and N:P ratio in seven forest herbs. The herbs were collected in the (experimental) populations of four ancient and four post-agricultural forest stands. See methods for details on model building.

	Effect	χ^2
N concentration		
	Land use	0.419
	Colonization capacity	0.385
	Biomass	1.400
P concentration		
	Land use	+ 9.542**
	Colonization capacity	2.315
	Biomass	1.646
N:P ratio		
	Land use	- 8.953**
	Colonization capacity	0.613
	Biomass	0.811

Notes: Effects were tested with linear mixed models including 'Forest stand' and 'Species' as non-nested random effect terms; the N and P concentrations were transformed by the natural logarithm. The χ^2 statistic is based on a likelihood ratio test between a full model and a model without the predictor variable. 'Land use' was coded as a binary variable (0: ancient; 1: post-agricultural), i.e., a positive effect indicates a higher value in post-agricultural versus ancient forest. **: $P < 0.01$

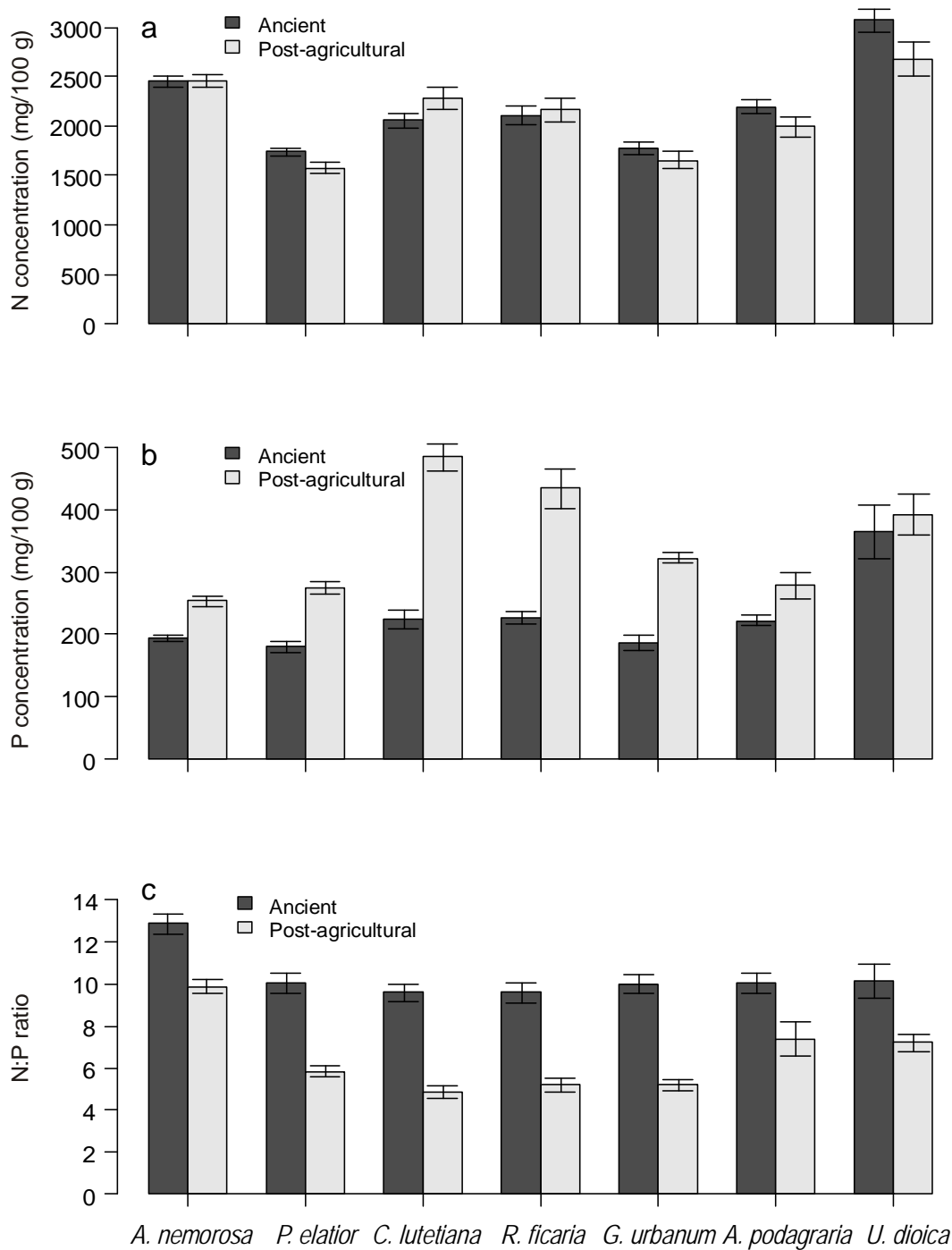


Fig. 1 Effect of land-use history on the N concentration (a), P concentration (b) and N:P ratio (c) for seven forest herbs (average \pm SE; N = maximum 40 per species). The herbs were collected in (experimental) populations of four ancient and four post-agricultural forest stands. The species were sorted according to their colonization capacity from left (slow colonizers) to right (fast colonizers). Results of the multilevel models are reported in Table 3

Six out of the seven forest herbs tended to increase their biomass in the post-agricultural stands relative to the ancient stands (Fig. 2). For four species, the difference was significant at the 0.1 level. Only *A. nemorosa* did not show a higher average biomass per ramet in post-agricultural compared to ancient forest stands. *Urtica dioica*, on the other hand, showed the strongest response to former land use and increased its average biomass by a factor c. 4 in post-agricultural stands. Finally, the degree to which the species increased their biomass in post-agricultural versus ancient forest stands was significantly related to the colonization capacity index, i.e., the slowest colonizers (high CCI) showed the smallest relative increase in biomass (Fig. 3).

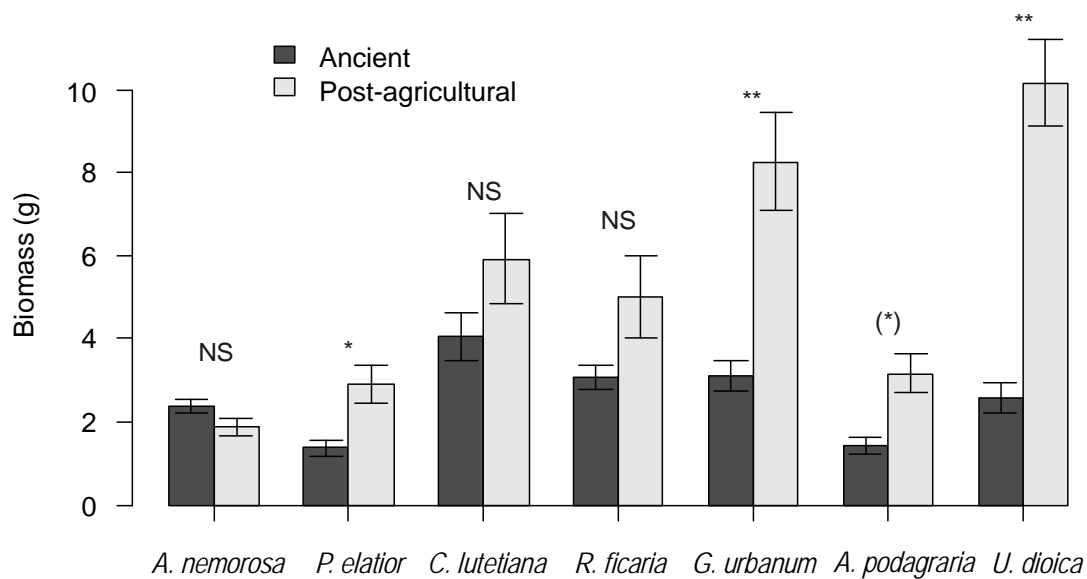


Fig. 2 Differences in the aboveground dry biomass of seven forest herbs in ancient and post-agricultural forest stands (average \pm SE; N = maximum 40 per species). The species were sorted according to their colonization capacity from slow colonizers (left) to fast colonizers (right). The biomass values for *A. nemorosa* and *R. ficaria* were rescaled to the biomass of 20 ramets and for *C. lutetiana* to 10 ramets. The effect of former land use was tested with multilevel models including 'Forest stand' as random effects term; NS: not significant; (*) $P < 0.1$; * $P < 0.05$; ** $P < 0.01$

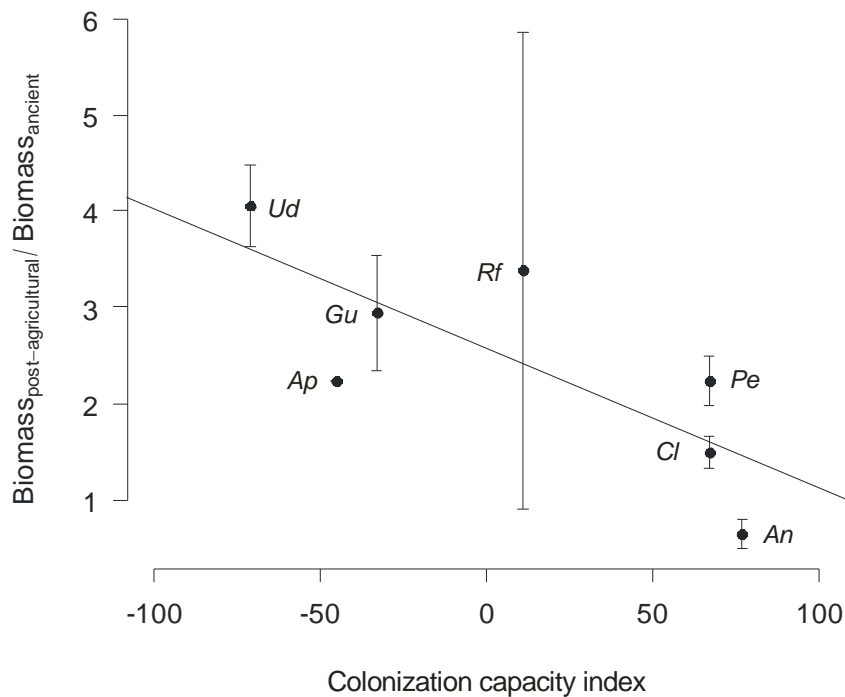


Fig. 3 Relation between the colonization capacity index (CCI) of the seven forest herbs and the ratio of their average biomass in post-agricultural versus ancient forest stands (averaged over the three forest sites). Slowly colonizing species have a high CCI value. The slope of the linear relation was significantly different from zero ($t = -2.714$; $P < 0.05$) with $R^2 = 0.515$

Discussion

Studies that determined the impact of land-use history on the forest herb layer have mainly focused on the distributional patterns of forest herbs and the degree to which dispersal and recruitment hamper their colonization (reviews: Flinn and Vellend 2005; Hermy and Verheyen 2007). Yet, once a forest herb has germinated, the former land use may also have effects on the performance of the forest herbs (e.g., Endels et al. 2004; Verheyen and Hermy 2004; Vellend 2005; Fraterrigo et al. 2006; Baeten et al. 2009a). The uptake of N and P forms a particular component of plant performance related to plant growth, but the issue has received little attention to date (Falkengren-Grerup et al. 2006; Baeten et al. 2009a). Here we showed that land-use history significantly affected the aboveground P concentrations and biomass of seven forest herbs with higher concentrations and biomass in post-agricultural stands. Land-use effects on nutrient concentrations were similar for slow and fast colonizing species, but the fast colonizers tended to increase their biomass more in response to the former agriculture compared to the slow colonizers.

Land-use effects on plant nutrient concentrations

The seven forest herbs showed consistently higher P concentrations in their aboveground biomass in the post-agricultural stands compared to the ancient stands. The higher aboveground plant P concentrations indicate that the former fertilization has increased the bio-available pool of soil P in the post-agricultural stands (Table 2), which is consistent with soil studies showing a remarkably persistent P enrichment in forests on former agricultural land (Koerner et al. 1997; Verheyen et al. 1999; De Keersmaecker et al. 2004; Falkengren-Grerup et al. 2006; Dambrine et al. 2007). Likewise,

Baeten et al. (2009a) showed that the contrasting land-use history of forest stands was reflected in the plant P concentrations of two forest herbs (*P. elatior*, *G. urbanum*). Furthermore, the plastic response of forest herbs to increased P availability we found here partly generalizes the results from pot experiments (Pigott and Taylor 1964; Hipps et al. 2005; Baeten et al. 2010) to field conditions and a larger set of species. The first hypothesis thus seems to hold regarding the plant P concentration.

The N concentrations, on the other hand, did not differ between plants in post-agricultural and ancient forest stands (cf. Baeten et al. 2009a). This lack of differentiation between the contrasting land-use histories may have principally two causes. First, the pool of plant available N might not strongly differ between the ancient and post-agricultural forest stands. Our soil data indicated that at least the total N pool does not depend on the historical land use of the sites (Table 2). Due to the high mobility and multiple loss pathways of mineral soil N (e.g., Schulze 2000), the legacy of past fertilization was probably only temporary, and the actual N state of the ecosystem is rather determined by factors such as soil type and humus, tree species composition and atmospheric N deposition loads (e.g., Compton et al. 1998; Gundersen et al. 2006). Second, the forest herbs may simply exhibit low plasticity in response to the variation in N availability because the nutrient is in excess at our sites. Previous experimental studies found that forest herbs may increase their foliar N concentrations and aboveground biomass with N fertilization (e.g., Elemans 2004; Fraterrigo et al. 2009), but not if N was not limiting plant growth (Tessier and Raynal 2003). Explanations for a potentially excess N availability at our study sites are the inherently high N availability in alluvial forest systems (e.g., through fast litter decomposition, alluvial inputs), which is supplemented with a high total inorganic N throughfall deposition (34–46 kg.ha⁻¹.yr⁻¹ in the Flemish ICP Level II monitoring plots between 1993 and 2002, Neiryneck et al. 2004).

There was substantial variation in plant N and particularly in plant P concentrations among the species (cf. second hypothesis), but the variation was unrelated to the capacity of the species to colonize post-agricultural forests. The third hypothesis is thus not supported by the data. Baeten et al. (2010) came to a similar conclusion for P in a pot experiment with four forest herbs: both slowly and fast colonizing species may exhibit high plasticity in response to P addition. In the present study, the variation in N and P concentration among species was also not related to differences in life form or phenology. It is therefore difficult to extrapolate our results to other study sites, which concurs with the findings of Fraterrigo et al. (2006). Thus, the responses to P availability seem to be largely species specific and related to individual life histories.

Because former land use had an effect on the uptake of P in the aboveground biomass of the forest herbs, but not on N uptake, the N:P ratios in the studied forest herbs strongly differed between post-agricultural and ancient stands. As the N:P ratio of the individual species was consistently lower in the post-agricultural stands, the vegetation-level N:P ratio is probably also reduced in those stands. Vegetation-level N:P ratios are commonly used as a practical tool to estimate the degree to which the community is limited by N availability (low N:P), by P availability (high N:P) or co-limited by both at intermediate N:P ratios (reviews: Tessier and Raynal 2003; Güsewell 2004). An important restriction to the application of N:P ratios to assess nutrient limitation, however, is that either N or P is a limiting resource for plant growth (Tessier and Raynal 2003). The relatively low N:P ratio in post-agricultural forest should therefore not be interpreted as an indication of N limitation at those stands, which would be very unlikely at our alluvial sites (see above).

The increased P concentrations and altered N:P ratios in the herbaceous species may have important implications for some key components of the ecosystem functioning. For instance, the herbaceous layer accounts for a considerable proportion of the total annual foliar litter fall (on average 10–15 %), and this herbaceous litter forms a particularly labile fraction of fast decomposing material (overviews in Muller 2003; Gilliam 2007). The higher P concentrations in the aboveground biomass of forest herbs may thus have a profound influence on the cycling of P. The community composition of the decomposers involved in the litter decomposition may additionally depend on the lower N:P ratio of the plant material. A microcosm experiment by Güsewell and Gessner (2009), for instance, showed that the relative importance of fungi decreases while bacteria are promoted at lower litter N:P ratios. Although herbivory may also interact with the nutrient availability and uptake by plants (Anderson 2003), this and other multitrophic interactions largely remain to be studied.

Land-use effects on aboveground plant biomass

Past land use had a substantial impact on the total aboveground biomass of most forest herbs. We acknowledge that total biomass is only a rough measure of plant performance, but it may be considered an integrated estimation of overall performance related to plant interactions (e.g., competition). The observation that the species mainly responded in terms of P, and not N uptake, at least suggests that of the two nutrients P is the one that may be partly associated with the increased biomass in the post-agricultural stands, especially if we assume N to be a non-limiting nutrient at our sites (see above). In a pot experiment with four of the species we sampled here, Baeten et al. (2010) found higher biomass production in response to P supply, but differences in light availability also had an effect. If land-use history affects the composition and structure of the canopy, e.g. with higher light availability in post-agricultural sites, this might also account for the observed plasticity in biomass production for species such as *U. dioica*, *A. podagraria* and *G. urbanum* (Pigott and Taylor 1964; Elemans 2004; Baeten et al. 2010). The relative importance of light availability was, however, not explicitly determined here.

There were also clear interspecific differences in biomass response to the former land use, and those differences were partly related to colonization capacity: the fast colonizing species were able to increase their biomass more than the slow species in post-agricultural versus ancient forest. Although the relation between the colonization capacity index and the relative biomass was not particularly tight (Fig. 3), it showed that the slow colonizing species not only suffer from lower dispersal and recruitment rates (Verheyen et al. 2003b; Baeten et al. 2009a, b), but additionally have a lower ability to benefit from the altered habitat quality. While *U. dioica* almost increased its biomass by a factor four in post-agricultural compared to ancient forest, the increase for *A. nemorosa*, *P. elatior* and *C. lutetiana* was smaller (maximum a factor 2.2). In this way, individuals of *U. dioica* (and *G. urbanum*) became much larger than the slow species in post-agricultural forest (e.g., the biomass of *P. elatior* individuals was on average 3.5 times lower). The strong response of *U. dioica* to former land use, and P in particular, has been found elsewhere and is expected to be a hindrance to the recruitment and growth of slow colonizing forest plants (e.g., Endels et al. 2004; De Keersmaeker et al. 2004; Baeten et al. 2009a). In high nutrient environments, vigorously growing tall species such as *U. dioica* are able to project their leaves above those of neighbouring individuals, which gives them a disproportionate advantage to compete for light (Craine 2009; Haultier et al. 2009). While previous research already provided evidence that the nutrient legacies in post-agricultural forests might hamper particular recruitment stages of slow colonizing forest species

(Baeten et al. 2009a, b), the present study shows that those species may additionally have the disadvantage of being less plastic in terms of biomass production compared to the fast colonizers. This may accentuate their low colonization abilities.

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References

- Aerts R, Chapin FS (2000) The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Adv Ecol Res* 30:1-67
- Anderson WB (2003) Interactions of nutrient effects with other biotic factors in the herbaceous layer. In: Gilliam FS, Roberts MR (eds) *The herbaceous layer in forests of eastern north america*. Oxford University Press, Oxford, pp 91-101
- Baeten L, Hermy M, Verheyen K (2009a) Environmental limitation contributes to the differential colonization capacity of two forest herbs. *J Veg Sci* 20:209-223
- Baeten L, Jacquemyn H, Van Calster H, Van Beek E, Devlaeminck R, Verheyen K, Hermy M (2009b) Low recruitment across life stages partly accounts for the slow colonization of forest herbs. *J Ecol* 97:109-117
- Baeten L, Vanhellefont M, De Frenne P, De Schrijver A, Hermy M, Verheyen K (2010) Plasticity in response to phosphorus and light availability in four forest herbs. *Oecologia* 163:1021-1032
- Bates D, Maechler M (2010) lme4: Linear mixed-effects models using Eigen and S4 classes. R package version 0.999375-33. [<http://CRAN.R-project.org/package=lme4>]
- Compton JE, Boone RD, Motzkin G, Foster DR (1998) Soil carbon and nitrogen in a pine-oak sand plain in central Massachusetts: Role of vegetation and land-use history. *Oecologia* 116: 536-542
- Craine JM (2009) *Resource strategies of wild plants*. Princeton University Press, Princeton
- Dambrine E, Dupouey JL, Laüt L, Humbert L, Thinon M, Beaufiglioli T, Richard H (2007) Present forest biodiversity patterns in France related to former Roman agriculture. *Ecology* 88:1430-1439
- De Keersmaecker L, Martens L, Verheyen K, Hermy M, De Schrijver A, Lust N (2004) Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). *Forest Ecol Manag* 188:291-304

- Elemans M (2004) Light, nutrients and the growth of herbaceous forest species. *Acta Oecol* 26:197-202
- Endels P, Adriaens D, Verheyen K, Hermy M (2004) Population structure and adult plant performance of forest herbs in three contrasting habitats. *Ecography* 27:225-241
- Falkengren-Grerup U, ten Brink DJ, Brunet J (2006) Land use effects on soil N, P, C and pH persist over 40-80 years of forest growth on agricultural soils. *Forest Ecol Manag* 225:74-81
- Flinn KM, Vellend M (2005) Recovery of forest plant communities in post-agricultural landscapes. *Front Ecol Environ* 3:243-250
- Fraterrigo JM, Pearson SM, Turner MG (2009) The response of understory herbaceous plants to nitrogen fertilization in forests of different land-use history. *Forest Ecol Manag* 257:2182-2188
- Fraterrigo JM, Turner MG, Pearson SM (2006) Previous land use alters plant allocation and growth in forest herbs. *J Ecol* 94:548-557
- Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience* 57:845-858
- Gundersen P, Schmidt IK, Raulund-Rasmussen K (2006) Leaching of nitrate from temperate forests – effects of air pollution and forest management. *Environ Rev* 14: 1-57
- Güsewell S (2004) N : P ratios in terrestrial plants: Variation and functional significance. *New Phytol* 164:243-266
- Güsewell S, Gessner MO (2009) N : P ratios influence litter decomposition and colonization by fungi and bacteria in microcosms. *Funct Ecol* 23:211-219
- Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science* 324:636-638
- Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson JE (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biol Conserv* 91:9-22
- Hermy M, Verheyen K (2007) Legacies of the past in the present-day forest biodiversity: A review of past land-use effects on forest plant species composition and diversity. *Ecol Res* 22:361-371
- Hipps NA, Davies MJ, Dodds P, Buckley GP (2005) The effects of phosphorus nutrition and soil pH on the growth of some ancient woodland indicator plants and their interaction with competitor species. *Plant Soil* 271:131-141
- Koerner W, Dupouey JL, Dambrine E, Benoit M (1997) Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *J Ecol* 85:351-358

- Muller RN (2003) Nutrient relations of the herbaceous layer in deciduous forest ecosystems. In: Gilliam FS, Roberts MR (eds) *The herbaceous layer in forests of eastern North America*. Oxford University Press, Oxford, pp 15-37
- Neiryck J, Genouw G, Coenen S, Roskams P (2004) Deposition and air quality in Flemish forest areas [in dutch]. Instituut voor Bosbouw en Wildbeheer, Geraardsbergen
- Pigott CD, Taylor K (1964) The distribution of some woodland herbs in relation to the supply of nitrogen and phosphorus in the soil. *J Ecol* 52:175-185
- Scheel KC (1936) Colorimetric determination of phosphoric acid in fertilizers with the pulfrich photometer. *Z Analytische Chemie* 105:256-269
- Schulze E-D (2000) *Carbon and nitrogen cycling in european forest ecosystems*. Springer-Verlag, Berlin
- R Development Core Team (2009) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria
- Tessier JT, Raynal DJ (2003) Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. *J Appl Ecol* 40:523-534
- Vellend M (2005) Land-use history and plant performance in populations of *Trillium grandiflorum*. *Biol Conserv* 124:217-224
- Vellend M, Verheyen K, Flinn KM, Jacquemyn H, Kolb A, Van Calster H, Peterken G, Graae BJ, Bellemare J, Honnay O, Brunet J, Wulf M, Gerhardt F, Hermy M (2007) Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. *J Ecol* 95:565-573
- Verheyen K, Bossuyt B, Hermy M, Tack G (1999) The land use history (1278-1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. *J Biogeogr* 26:1115-1128
- Verheyen K, Guntenspergen GR, Biesbrouck B, Hermy M (2003a) An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale. *J Ecol* 91:731-742
- Verheyen K, Hermy M (2004) Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. *J Veg Sci* 15:125-134
- Verheyen K, Honnay O, Motzkin G, Hermy M, Foster DR (2003b) Response of forest plant species to land-use change: A life-history trait-based approach. *J Ecol* 91:563-577
- Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York