Original article

Broom (*Cytisus scoparius*) colonization after grazing abandonment in the French Massif Central: impact on vegetation composition and resource availability

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ABSTRACT

Broom (*Cytisus scoparius*) is considered an invasive species in countries outside its native range and a significant colonizing species in Europe. In particular this shrub rapidly invades pastures after grazing cessation in central France mid-elevation mountains. In order to better understand the effects of broom plants on vegetation composition and species richness after grazing abandonment, a study was conducted including stand descriptions and impact on light availability and soil properties. A total of 50 plots were sampled from the following categories: grazed pasture free of broom colonization, abandoned pasture in the process of being colonized by broom plants (1–3 years old), intermediate broom stand (2–4 years old), mature broom stand (4–5 years old) and dead broom stand (8–10 years old). In each plot the vegetation composition was measured; additionally, broom size and density were recorded. Light transmittance was measured beneath the broom canopy. Soil moisture, soil carbon (C), soil nitrogen (N), and nitrate production were measured in a subset of plots. Results showed that broom colonization is associated with a decline in species richness and cover, with a shift toward fast-growing species in the understory compared to uninvaded abandoned pasture. After broom decay stands were dominated by *Rubus* sp. plants. Concomitant to broom colonization and vegetation changes, light was severely reduced as only 11% of the incident light reached the floor in mature broom stands. In contrast soil moisture, N and C contents increased, respectively, of 37%, 52% and 61% in the upper soil layer from uncolonized pasture to mature broom stands and nitrate production was multiplied by 6.5. However changes in $\delta^{15}N$ values were not significant. Dead broom stands were characterized by lower values of N, C, and N mineralization as compared with the other types of broom stand. Our data suggest that land abandonment and broom colonization is associated with altered vegetation composition and resource availability and that this shrub tends to occupy a mid-successional position between early successional communities such as heathlands and grasslands and late-successional woodlands.

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1.   Introduction

Broom (*Cytisus scoparius* L.) is a commonly invasive species outside Europe having been introduced accidentally or on purpose into many countries (Williams, 1981; Waterhouse, 1988; Bossard, 1991; Fogarty and Facelli, 1999). Many features explain the ability of this leguminous shrub to successfully invade habitats outside its native range: long-lasting seed bank (Turner, 1933), early and massive seed production (Paynter et al., 2000), rapid growth and an ability to settle after a disturbance such as fire, logging or grazing abandonment (Fogarty and Facelli, 1999). Broom is capable of forming rapidly dense and monospecific stands and then overtopping and replacing the vegetation of natural or semi-natural ecosystems. Such modifications induce marked shifts in the relative abundance of native biota and can deeply alter the nature and functioning of invaded ecosystems (Waterhouse, 1988; Smith, 1994; Parker et al., 1999; Wearne and Morgan, 2004). The species is also a nuisance to livestock and a competitor for planted conifer seedlings (Peterson and Prasad, 1998; Watt et al., 2003b).

Within its native range and especially in central France broom was considered as a minor weed and this plant has been for centuries associated with agricultural practices and used to restore soil fertility after cultivation and also as fuel wood (Bazin et al., 1983; Rousseau and Loiseau, 1987). However, the decline of grazing over the last several decades has led to broom colonization in many open areas in which this shrub was previously controlled by cattle. As a consequence increasing floristic-rich grasslands are at now at risk of broom colonization, although no studies, to our knowledge, have examined the impact of broom on vegetation change within its native habitat.

It is noticeable that, unlike the dynamics of the shrub outside its native area, broom does not exhibit the same capacity to colonize very different habitats (from open grasslands to forests) and to form stable stands in Europe. Moreover broom colonization within its native range is associated with disturbances of grazing regimes, frequently occurring in moderately-grazed pastures and fallow lands (Rousseau and Loiseau, 1987). Several factors have been proposed to explain invasion and persistence of broom outside its native range:

- a lower abundance of specialist phytophages in exotic compared to native habitats (Memmott et al., 2000);
- greater longevity in introduced range (but see Paynter et al., 2003);
- increased capacity to regenerate in introduced range (Sheppard et al., 2002).

The aim of our study was to document the effects of broom colonization after grazing abandonment in central France on vegetation composition and species richness at different stages of the process: from the grazed pasture to the different stages of the colonization by broom plants. Soil properties and light availability were quantified for these different stages as it appeared important to us to understand how above and below ground resources were modified by this invading shrub, and how those changes could affect the community that followed broom stands after decay. Previous studies have shown that colonization by shrubs or trees often led to a drastic reduction of light availability and also altered C and N pools and dynamics (Archer et al., 2001; Lett and Knapp, 2003; Siemann and Rogers, 2003). N-fixing species were reported to induce a significant increase in N in soil within a short period (Vitousek, 1982; Vitousek and Walker, 1989; Shumway, 2000) and a significant increase in organic matter was also recorded for broom stands (Diquélou and Rozé, 1999; Haubensak and Parker, 2004). These data will also aid in a critical test of whether *Cytisus* behaves differently, or essentially the same, in its native and introduced ranges.

2.   Material and methods

2.1.   Study area and sampling design

The study area is located in the Chaîne des Puys (45°38′–45° 55′N and 2°47′–3°4′E), a volcanic mountain range of the French Massif Central, at a mean altitude of 1000 m. The climate in this area is mountainous with oceanic influences, mean rainfall is 1070 mm well spread thorough the year, and mean annual temperature is about 8 °C. The substratum of the studied site is composed of a granitic saprolite mixed with a small content (< 5% in volume) of volcanic ash deposits (trachytic tephras) (Camus et al., 1991) and exhibit some characteristics of andic soils (Prévosto et al., 2004).

The area (total 62 ha) is composed of grasslands grazed by domestic animals and mainly dominated by species of the *Nardo-Callunetea* and *Molinio-Arrhenatheretea* taxa such as *Deschampsia flexuosa*, *Nardus stricta*, *Holcus lanatus*, *Plantago lanceolata*. Broom regularly invades the grasslands due to insufficient and irregular grazing leading to a patchy vegetation structure. This particular structure allows us to sample chronosequences also defined as 'space-for-time' substitution (Pickett, 1989).

We selected six broom patches in this area in similar site conditions and free of grazing. Each patch is composed of mature broom plants at its center (4–5 years) and of younger plants at its edge (from 1 to 4 years). We ran six transects of about 36 m long from the uncolonized grasslands to the center of the patches. For each transect, we established a 4 m² plot at regular interval of 6 m. According to broom cover abundance, age and dimensions of broom plants, plots were separated in the following categories: mature and old stands, intermediate and young broom stands and, abandoned pasture (Table 1). In addition eight plots were established in a neighboring pasture still grazed by cattle and almost entirely free of broom colonization. Senescent stands were not found in the sampled patches and eight plots were established within eight different dead broom stands located in the proximity of the other broom stands (< 150 m). They are characterized by the absence of living broom plants and presence of scattered large old dead shrubs. However, they do not belong to the same continuum as the previous patches and so the conditions in which they established are not precisely known.

	Total number	Number of sampled soils	Age range (year)	Broom cover (%)	Height (m)	Basal area (m²/ha)	Density (stem per m²)
Grazed pasture (GP)	8	5	1–2	< 5	< 0.7	< 1	< 1
Abandoned pasture (AP)	8	6	1–3	23 (0–35)	0.77 (0.58–1.07)	2.4 (0.6–6.0)	4.2 (0.3–8.5)
Intermediate broom stands (IB)	18	10	2–4	78 (40–90)	1.31 (0.67–1.76)	16.5 (5.1–30.6)	29.4 (11.8–85.6)
Mature broom stands (MB)	8	6	4–5	100 (100–100)	2.56 (2.08–2.83)	39.1 (22.1–57.4)	14.1 (7.0–24.3)
Dead broom stands (DB)	8	6	8–10				

Table 1 – Plots characteristics by colonization stages. Values shown are means followed by the range in brackets

2.2. Vegetation measurements

On each plot all living broom plants regardless of size were counted and their diameter at stem base recorded with an electronic caliper (± 0.01 mm). Stem diameter of broom has been shown to be strongly related to plant biomass within the study area (Prévosto et al., 2004). Height of five plants randomly chosen in the plot was recorded and age was estimated by tree ring counting (Table 1).

All vascular species and terricolous mosses were recorded on each plot and each species was given a value of abundance-dominance according to the procedure of Braun-Blanquet (1932). Plant diversity was evaluated by computing three classical indices: the total number of species, the Shannon's index and the evenness index (see for instance Booth et al., 2003 for details on these indices).

2.3. Light and soil water content measurements

In broom colonized plots, photosynthetically active radiation (PAR, 400–700 nm) was measured at four locations using a linear ceptometer (Decagon Devices, Pullman, USA). Measurements were done simultaneously above and below the living broom canopy using an external sensor three times in the summer of 2003 at the same time and with a blue sky. Light transmittance for each stand was then computed from the ratio between the mean PAR values measured above and below broom cover.

Volumetric soil water content of the upper layer (0–15 cm) was measured using a TDR probe (TRIME device, IMKO) in 20 plots evenly distributed in the following categories: abandoned pasture, intermediate, mature and dead broom stands at four locations per plot. Measurements were taken during 6 consecutive weeks over a dry period of May and June 2003.

2.4. Soils sampling and analysis

On a subset of the plots (Table 1), soil samples were collected, during a dry day of early Spring 2004, at three points 0.3 m apart in the center of the plot and at two depths (0–15 and 15–30 cm) by using a single root auger of a constant volume (external dimensions 15 cm × 7.5 cm). Ground vegetation and the thin litter layer were removed prior to sampling. Soil subsamples in each plot were combined for each depth, immediately weighed and sieved through a 4 mm sieve. Soil moisture was measured by drying an aliquot at 105 °C in the laboratory and bulk density was calculated from the results (soil dry mass/volume). Air-dried samples sieved < 1 mm were analyzed chemically as follows: pH in water, total nitro-

gen content (Kjeldahl's method), total carbon content (oxidation by $K_2CR_2O_7$ in H_2SO_4, Duchaufour, 1983). In addition, variation in ^{15}N natural abundance in soils was measured. After grinding to < 50 μm the natural abundance of ^{15}N was determined in subsamples by mass spectrometry (FINNIGAN DELTA S). Results are expressed in ‰ deviation from the international standard atmospheric N_2 ($\delta^{15}N$ = (Rsample/Rstandard – 1) × 1000 where R = $^{15}N/^{14}N$) (Mariotti, 1983). By convention the value is 0‰ for the atmosphere.

In order to assess the impact of broom cover on nitrate and ammonium production and N mineralization, soils, sieved through a 4 mm sieve, were incubated aerobically immediately after sampling in the field. For each sampled plot, two subsamples of 400 g of soil (0–15 and 15–30 cm) were placed in hermetic plastic boxes to avoid evaporation and kept at a constant temperature (T = 18 °C) and a constant humidity level (45% g water/g dry soil) for 3 weeks. These conditions were selected because they represented approximately soil moisture and temperature measured in the field when sampling. Water contents were obtained either by adding water to the initial content or by gently drying the soils at room temperature. Mineral nitrogen (NH_4 and NO_3) contents extracted by K_2SO_4 0.5 M (20 g soil/20 g solution) were measured with an automatic colorimeter (TRAACS 2000) at three dates $t_0 = 0$ (initial measurement before incubation), t_1 = 10 days and $t_2 = 21$ days.

2.5. Data analysis

From the vegetation data, a floristic array was established after eliminating species represented by ≤ 2 occurrences. Then, a factorial correspondence analysis (Greenacre, 1984), was undertaken using ADE-4 software (Thioulouse et al., 1997). This method extracts axes that maximize the dispersion of vegetation data and it has proven efficient for ordering sites according to species composition (Ter Braak, 1985). Differences between stands in the vegetation and soil variables were tested with one-way ANOVA followed by Tukey's multiple range test. ANOVA was preferred to regression equations using for instance stand density or biomass as predictors as it enabled us to compare all types of stands including grazed pastures and dead broom stands both characterized by a null density and biomass. By contrast, light transmittance was also given as function of broom basal area or broom height as it is usually done in forest stands (Sonohat et al., 2004). All statistics were produced using Statgraphics software (v. 5.1 Statistical Graphics Corp.).

3. Results

3.1. Change in vegetation composition

There was a large variation of vegetation composition as shown in the factorial correspondence analysis (Fig. 1). The horizontal axis separates clearly plots established in the grazed pasture from the other plots, and so reflects vegetation change due to grazing cessation. In particular the absence of grazing was correlated with the strong decline or disappearance of species specifically related to extensively grazed pastures in our area such as *Senecio adonidifolius*, *Festuca nigrescens*, *Potentilla heptaphylla*, *Hieracium pilosella*.

The second axis of the factorial correspondence analysis depicts vegetation changes due to broom colonization. It distinguishes plots of the abandoned pasture (above the horizontal) from plots located in the mature and dead broom stands (below the horizontal) while plots of other younger broom stands occupy an intermediate position. The greatest differences in the composition of the vegetation as depicted by this axis were found in the increase of ligneous species and of species with nitrophilous tendency: *Rubus fruticosus*, *Rubus idaeus*, *Holcus mollis* in particular. Most common spe-
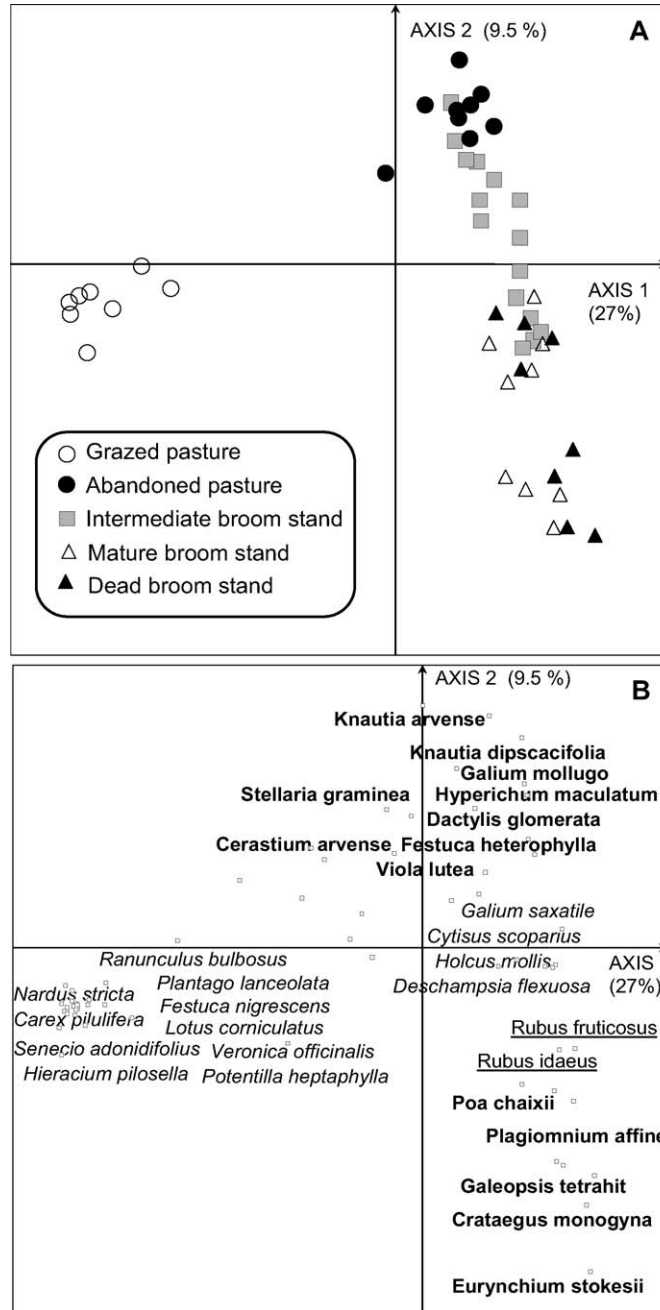

Fig. 1 – Projection of the plots A) and of the species B) on the two first FCA axes (eigenvalues $\lambda_1 = 0.606$, $\lambda_2 = 0.213$). Species whose contributions are greater than the mean contribution are indicated in italics for the first axis, in bold for the second axis and are underlined for a contribution on both axes.

	Grazed pasture	Abandoned pasture	Intermediate broom stand	Mature broom stand	Dead broom stand
Table 2 – Mean frequency and diversity indices mean values of the different taxonomic groups for the different colonization stages. Within each row, different lower case letters indicate statistically significant differences (P < 0.05)					
Nardo-Callunetea and *Molinio-Arrhenatheretea* (%)	42.9 (a)	37.7 (a, b)	30.3 (b, c)	24.8 (b, c)	18.3 (c)
Querco-Fagetea (%)	6.9 (a)	17.9 (b)	15.2 (b)	16.0 (b)	16.4 (b)
Indifferent species (%)	12.6 (a)	20.6 (a, b)	25.9 (b, c)	36.2 (d)	32.3 (c, d)
Rubus sp. cover (%)	0.0 (a)	1.9 (a)	24.9 (b)	22.7 (b)	53.2 (c)
Number of species	30.1 (a)	16.8 (b)	15.3 (b)	11.2 (c)	10.5 (c)
Shannon index	2.78 (a)	2.11 (b)	2.04 (b)	1.73 (c)	1.61 (c)
Evenness index	0.68 (a)	0.51 (b)	0.50 (b)	0.42 (c)	0.39 (c)

cies of open grasslands also declined such as *Knautia* sp., *Cerastium arvense*, *Viola lutea*, *Stellaria graminea*.

The change in vegetation composition is also depicted in Table 2. Grazing abandonment and then broom establishment led to a decrease of the *Nardo-Callunetea* and *Molinio-Arrhenatheretea* groups. In contrast the increase of the forest species belonging to the *Querco-Fagetea* group was only significant between the grazed and the abandoned pasture. The development of *Rubus* cover was particularly noticeable as this species was absent or weakly developed in the grazed and abandoned pastures but strongly developed with broom colonization becoming dominant after broom decay.

Plant diversity indices all indicated that plant diversity was maximal in the grazed pasture due to the presence of light-demanding species tolerant to grazing. On the other hand diversity indices dramatically decreased after abandonment followed by broom colonization reaching a minimum in dead broom stands dominated by *Rubus* sp.

### 3.2. Impact of broom on light and water availability

Radiation transmittance was strongly and negatively correlated with basal area (Fig. 2). Light availability was maximal in pastures free of broom colonization but rapidly declined with broom colonization (Table 3). As a consequence, only 11% of the incident light reached the ground in mature broom stands. Senescence due to age leads to a rapid

decrease of broom cover and the restoration of full light conditions. Due to the absence of senescent stands in our study area (i.e. mature brooms still alive but showing symptoms of decay), the restoration of full light conditions due to senescence was not measured in the field and only the supposed light regime was represented in Fig. 2.

Soil water content was significantly higher under the complete cover of mature broom stands than under the partial cover of intermediate broom stands or in the absence of broom colonization (Fig. 3). Dead broom stands completely colonized by *Rubus* species show values comparable to mature broom stands.

3.3. Impact on soil fertility

Bulk density of the upper layer was significantly higher for the grazed pasture than the other colonization stages (Table 3). In contrast, bulk density was homogeneous in the 15–30 cm soil layer regardless of the colonization stage. Soil moisture significantly increased and pH significantly decreased with broom colonization in the surface soil, but in the deeper soil layer differences were not significant. C and N contents in the upper layer increased from the grazed to the abandoned pasture and then from the abandoned pasture to the mature broom stands but decreased in dead broom stands. The trend was similar in the 15–30 cm layer but variations were less marked. C and N stocks were only
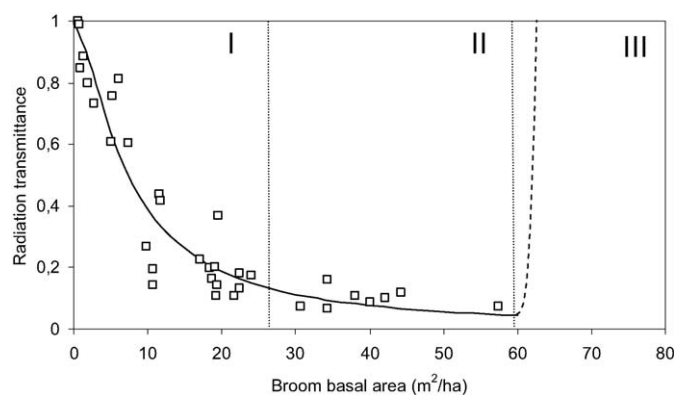
Fig. 2 – Radiation transmittance measured below ground canopy as a function of broom basal area. I) Abandoned pastures and intermediate broom stands II) mature broom stand III) broom decay and restoration of full light conditions. The solid line indicate the regression curve $y = 1/(1 + 0.0526 \times x^{1.4743})$ $R^2 = 0.91$. The dash line represents the estimated radiation transmittance following broom senescence and the restoration of the full light conditions.

Table 3 – Light availability and soil characteristics according to the different colonization stages. Within each row, different lower case letters indicate statistically significant differences ($P < 0.05$)					
	Grazed pasture (GP)	Abandoned pasture (AP)	Intermediate broom stands (IB)	Mature broom stands (MB)	Dead broom stands (DB)
Light transmittance ratio (below/above)	1 (a)	0.85 (a)	0.26 (b)	0.11 (c)	Not measured ≈ 1
Bulk density (g/cm^3) 0–15 cm	0.93 (a)	0.62 (b)	0.58 (b)	0.62 (b)	0.68 (b)
Bulk density (g/cm^3) 15–30 cm	1.02 (a)	0.98 (a)	0.89 (a)	0.90 (a)	1.01 (a)
Soil moisture (%) 0–15 cm	39.7 (a)	45.3 (a)	48.6 (a, b)	54.3 (b)	46.9 (a, b)
Soil moisture (%) 15–30 cm	46.0 (a, b)	42.4 (a)	43.3 (a)	51.8 (b)	41.5 (a)
pH 0–15 cm	5.15 (a)	4.61 (b)	4.44 (c)	4.50 (b, c)	4.36 (c)
pH 15–30 cm	5.31 (a)	4.73 (b)	4.75 (b)	4.76 (b)	4.59 (b)
C (%) 0–15 cm	7.56 (a)	9.50 (b)	11.12 (c)	11.52 (c)	8.49 (a, b)
C (%) 15–30 cm	4.97 (a)	5.31 (a)	5.65 (b)	7.06 (b)	4.89 (a)
N (%) 0–15 cm	0.64 (a)	0.89 (b, c)	1.04 (c)	1.03 (c)	0.81 (a, b)
N (%) 15–30 cm	0.41 (a)	0.49 (a, b)	0.49 (a, b)	0.58 (b)	0.44 (b)
C stock (1000 kg/ha) 0–30 cm	139.42 (a)	134.18 (a)	131.34 (a)	163.02 (b)	133.97 (a)
N stock (1000 kg/ha) 0–30 cm	11.68 (a)	12.36 (a, b)	11.88 (a)	13.97 (b)	12.33 (a, b)
δ^{15}N (‰) 0–15 cm	4.09 (a)	3.32 (b, c)	2.83 (c)	3.14 (b, c)	3.85 (a, b)
δ^{15}N (‰) 15–30 cm	5.97 (b)	5.49 (a, b)	5.03 (a)	5.31 (a, b)	5.32 (a, b)
N-NH$_4$ initial (mg/kg) 0–15 cm	0.93 (a)	0.93 (a)	0.84 (a)	0.78 (a)	0.61 (a)
N-NH$_4$ initial (mg/kg) 15–30 cm	0.59 (a)	0.66 (a)	0.69 (a)	0.72 (a)	0.69 (a)
N-NO$_3$ initial (mg/kg) 0–15 cm	0.30 (a)	2.36 (b)	3.93 (c)	3.51 (b, c)	2.30 (b)
N-NO$_3$ initial (mg/kg) 15–30 cm	0.30 (a)	1.25 (a, b)	2.02 (b, c)	2.72 (c)	1.83 (a, c)
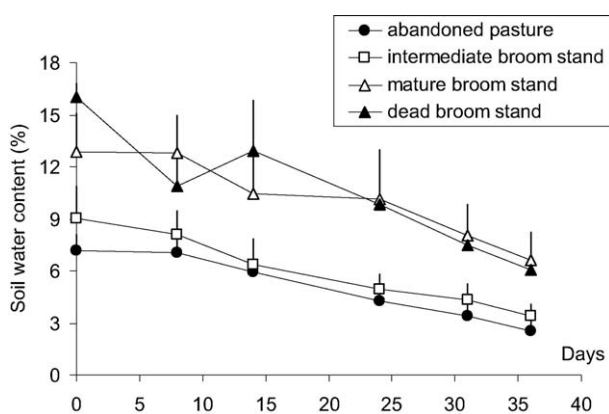
Fig. 3 – Soil water content (mean + S.E.) according to the different categories during a dry period of summer 2003 (from 20/05 to 25/06).

significantly higher in the mature broom stands. In fact, variations were buffered because of the balance between decreased bulk density and increased C, N contents. Lastly, C content was strongly and positively related to soil moisture ($R^2 = 0.63$, $F = 52.9$, $P < 0.001$), negatively and weakly related to pH ($R^2 = 0.25$, $F = 10.4$, $P < 0.05$), and strongly and negatively related to bulk density ($R^2 = 0.66$, $F = 58.8$, $P < 0.001$) as recorded in a previous study in the same area (Prévosto et al., 2004).

The δ^{15}N values were expected to decrease with N fixation by broom. Although there was a significant decrease from grazed to abandoned pasture, values recorded in broom stands were not significantly different from the abandoned pasture values.

There were no significant differences in N-NH$_4$ initial content (Table 3) but N-NO$_3$ initial content significantly increased with the colonization stages. Dead broom stands were characterized by a significant lower nitrate content (Table 3). Changes are more marked in the first than in the second layer. N mineralization produced mostly NO$_3$ form. Nitrate production increased with time and was always higher in the first soil layer (Fig. 4). There was a large increase in nitrate production from the grazed to the abandoned pasture followed by a moderate increase linked to broom establishment (Fig. 4). A decrease in nitrate production was observed from the mature to the dead broom stands.
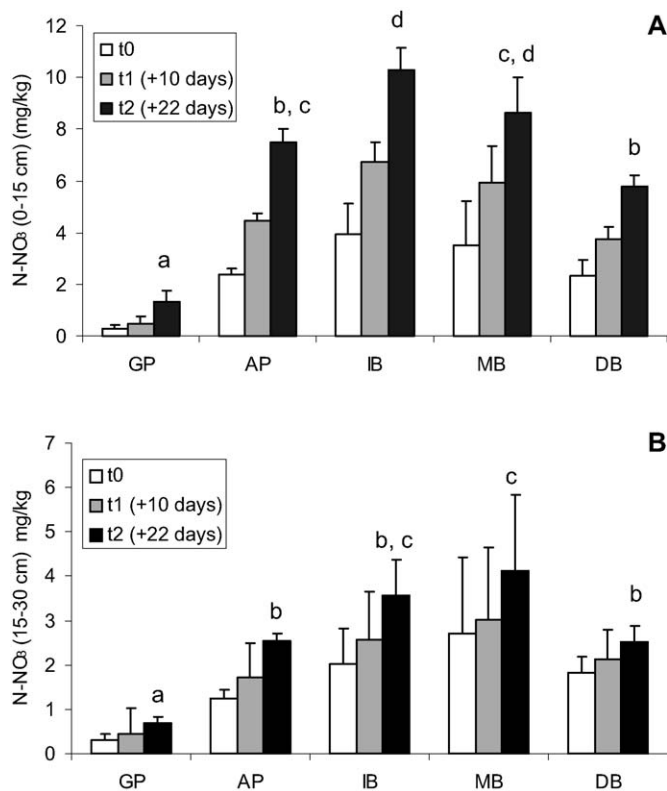
Fig. 4 – Effect of colonization stage on nitrate production over time for soil at depth of A) 0–15 cm and B) 15–30 cm. Symbols of the *x*-axis indicate: GP, grazed pasture; AP, abandoned pasture; IB, intermediate broom stands; MB, mature broom stands; DB, dead broom stands. Different lower case letters indicate statistical differences ($P < 0.05$) at time t_2.

4. Discussion

4.1. Impact on vegetation composition

Vegetation changes recorded in this study were explained by two major disturbances: grazing abandonment and broom canopy closure. There was a first significant shift in vegetation composition due to grazing abandonment: a decrease in species diversity and an increase in nitrophilous tall herbs and grasses such as *Silene vulgaris*, *Knautia arvensis*, *Poa pratensis* and a large development of *Holcus mollis*. This finding is in line with the results found in previous studies that have recorded diversity alteration after grazing abandonment (Willems et al., 1993; Dzwonko and Loster, 1998; Dupré and Diekmann, 2001; Krahulec et al., 2001). This can be explained by the fact that grazing usually enhanced species diversity by favoring weakly competitive plant species at the expense of tall competitors (Krahulec et al., 2001; Dupré and Diekmann, 2001). In fact, grazed sites had higher proportions of small species and species with basal positions of leaves (e.g. *Hieracium pilosella*, *Plantago lanceolata*) indicating that grazing favored some life-traits of species different from those recorded in case of abandonment (Dupré and Diekmann, 2001). It is noteworthy that within our study area several species of high ecological value were confined to grasslands and were suppressed by the plants that became dominant after abandonment. In fact, some of these species

characterized by weak competition abilities, are also favored by the pastoralism because of whether their toxicity or their indigestibility (e.g. *Senecio adonodifolius*). The selection pressure they undergo is then reduced and result in an enhancement of their fitness.

Then there was a second marked alteration in composition and abundance of the ground vegetation due to broom canopy closure concomitant with soil enrichment. Due to shrub development, most of the light-demanding species disappeared. As a consequence, species number and species cover were particularly low under mature broom stands. Only a few herbaceous species (e.g. *Holcum mollis*, *Poa chaixii*, *Deschampsia flexuosa*) or ligneous species (*Rubus* sp.) can persist beneath the fully developed broom canopy. Similarly, Wearne and Morgan (2004) recorded a strong decrease in species richness after broom colonization in subalpine vegetation in Australia due to 95% reduction in light under broom canopy. However these authors noted no establishment by any shade-tolerant species whereas *Rubus*, in our study, fully benefited from the return of full light conditions and became dominant after broom decay.

4.2. Light and water changes due to broom colonization

Reduced light in the broom understory had two major effects. First, it prevented broom seedlings from successfully establishing because no seedlings were recorded beneath closed canopy. Williams (1981) showed experimentally that

broom seedlings have reduced growth and vigor under low light conditions similar to those prevailing in mature broom understory. Second, reduced light induced a fast vegetation change as explained above. It is noteworthy that light reduction from full light conditions to about 11% occurred in a very brief period (< 4 years) in the case of high broom recruitment.

Concomitant to light reduction, soil moisture was also modified by broom colonization as it was higher beneath the broom canopy than in the grasslands. The beneficial impact of woody shelter on the soil moisture regime can be explained by the reduced evapotranspiration of the soil surface due to shade not balanced by the transpiration of broom plants. Stem flow may also concentrate water underneath shrubs or hydraulic lift may move water from deep in the soil profile to upper soil layers (Scholes and Archer, 1997).

4.3. Impact on soil properties

Soil properties were significantly modified by grazing abandonment before broom colonization occurred. Grazing is known to influence N mineralization and alter soil compaction by trampling (Bardgett et al., 1998). Soil decompaction resulted in a large decrease of soil bulk density between grazed and abandoned sites (from 0.93 to 0.62 g/cm^3) which explains the increase in C, N contents and in N mineralization. Actually, a high bulk density can have a detrimental effect on N mineralization because of increased physical protection of organic materials from mineralization processes due to a reduction of soil porosity (Breland and Hansen, 1996). Sampling procedure can also explained such variations. As C concentration usually decreases with depth, the comparison of fixed depth soil layers can result in an apparent increase in soil C content where soil density is the lowest (Moares et al., 2001). Grazing exports nitrogen, reduces the return of litterfall and the accumulation of litter, thereby reducing mineralization rates (Hobbie, 1992; van Wijnen et al., 1999). Grazing can also favor nutrient-conservative species whereas the nitrophilous species that establish after abandonment can input more C and nutrients into the soil system (van der Krift and Berendse, 2002).

Broom thicket-formation was associated with increased N content and increased nitrification, a common feature recorded in the case of invasion by N-fixing species (Ehrenfeld, 2003). Diquélou and Rozé (1999), studying soil properties after broom colonization in Brittany, France, demonstrated a fast and significant rise in soil N microbial biomass, organic matter content, microbial activity and especially in N-NO$_3$. These authors recorded an N-NO$_3$ content that was 8–13-fold higher in broom thickets than that in grasslands and croplands. However, they did not measure the variation in soil bulk density and the selected grasslands and croplands were abandoned for only 1 year. Similarly, Haubensak and Parker (2004) studying soil changes due to broom invasion in glacial outwash prairies of western Washington in the US reported 2.4 times greater nitrification rate in soils invaded by broom compared to uninvaded soils. Increased N content was explained by atmospheric N fixation by Rhizobium sp. symbiosis and litter restitution to the soil, the broom plant being an effective fixer in N poor soils (Watt et al., 2003a). The high nitrate production resulting

from nitrification can also lead to nitrate leaching and then to soil acidification (van Bremen et al., 1984). This could explain the decreasing pH values from open areas to broom stands.

Broom colonization also increased the C pool. The mechanisms accounting for this process can be identified in litter accumulation followed by fast decomposition in tissue chemistry and root distribution and in changes in the mass and species composition of the soil biota (Ehrenfeld, 2003; Archer et al., 2001).

It is noteworthy that dead broom stands were characterized by lower N and C contents and stocks (Table 3). One explanation is that the exact age of decay and conditions in which these stands established and grew were not known. Fluctuations of grazing could have produced stands of lower density and therefore the impact on soil C and N dynamics could have been lessened. It is also possible that the colonization and persistence of the nutrient-demanding red raspberry and blackberry after broom decay could have decreased the N and C pools. Due to these limitations it is not possible to conclude how long the effects of broom colonization on soil C, N dynamics persist after broom decay.

The δ^{15}N decreased from grazed to abandoned pastures and then did not show significant variation with broom colonization. Similarly, Haubensak and Parker (2004) did not find significant differences in δ^{15}N values of soils across transects from uninvaded grassland to broom stands in the US. Along with these authors, this probably indicated that mineral uptake in broom stands can be more important than N$_2$-fixation especially in our not N-depleted soils. It is noteworthy that in the literature N$_2$-fixing is not systematically correlated with variation in ^{15}N natural abundance (Hansen and Pate, 1987; Binkley et al., 1985).

4.4. Comparison of broom dynamics within and outside its native range

Within our study area, broom stands established on abandoned pastures tend to be fairly uniform in age (Prévosto et al., 2004), although some stands exhibit a more irregular structure on former heathlands (Rousseau and Loiseau, 1987; Paynter et al., 2003). Under the closed canopy of these regular stands, usually no broom seedlings successfully established (Paynter et al., 1998; Paynter et al., 2000; Prévosto et al., 2004). In contrast, in exotic habitats broom recruitment was not reduced by the presence of an established stand, thus allowing stands to persist even in absence of disturbance (Downey and Smith, 2000; Sheppard et al., 2002). The absence of regeneration within our study area could be explained by the replacement of broom stand by a competing ground vegetation composed of ligneous and semi-ligneous species (Table 2), a process that was apparently not observed in exotic habitats (Wearne and Morgan, 2004). Among the species that successfully established after broom decay, Rubus fruticosus and Rubus idaeus played a major role in this study in explaining the failure of broom seedlings to successfully establish after broom stand decay although additional experimental studies are needed to clearly establish the role of this competing vegetation on broom seedling establishment in old broom stands. These species were known to

invade rapidly disturbed forest ecosystems (Marks and Bormann, 1972), to benefit from nitrogen enrichment (Jobidon et al., 1989; Tilman, 1987) even under a plant canopy (Jobidon, 1993) and to rapidly develop with increasing light availability (Ricard and Messier, 1996; Lautenschlager, 1997; Mayer et al., 2004). Being particularly competitive, the large and fast increase of these species covers after the return of full light conditions due to broom decay could have prevented any further broom seedling establishment. Similarly, nitrogen-fixing legumes have been shown to increase soil nitrogen levels and to facilitate seedling growth in other successional communities (Morris and Woods, 1989; Vitousek and Walker, 1989). It was noteworthy that there was a correlation of *Rubus* sp. expansion and some tree and ligneous shrub species. In Brittany (western France), tree species are also reported to establish some decades after broom colonization of old fields (Diquélou and Rozé, 1999).

4.5. Management of broom stands in central France

Our results along with those found by Diquélou and Rozé (1999) in western France and indications given by French flora (Rameau et al., 1993) tended to indicate that this shrub occupied a mid-successional position between early successional communities such as heathlands and grasslands and late-successional woodlands. From this consideration, management of broom vegetation can be viewed in two ways. Broom management can first tend to the reversal of such succession: eradication of broom by mechanical means followed by grazing is commonly practiced in our study area and allows the restoration of the grassland. However, this method is money and time consuming and the resulting community may not be the one that is expected although this particular point has to be studied in detail. As land abandonment is frequent due to insufficient grazing another possible way of management could consist in the anticipation of the dynamics by tree planting. Broom can compete with tree seedlings for water and light (Watt et al., 2003b). However, broom also prevents the development of a dense ground vegetation of monocotyledons that is particularly damaging for tree growth (Nambiar and Sands, 1993) and responsible for many failures in tree plantations in our area (Frochot et al., 1986). Broom decay occurs at the age of 8–10 years and the decomposition of the woody material as well as the soil enrichment recorded in this study could also enhance tree growth after the juvenile stage (Watt et al., 2003a). Introduction of late-successional tree species such as *Fagus sylvatica* L., whose plantations are avoided in full light conditions, could also be a suitable and a cost-effective target in many parts of the French Massif Central and other areas although further studies are needed to determine more precisely the competitive interactions in juvenile stages between the shrub and the target species.

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