Changes of Humus Features along with a Successional Gradient of Rhododendron ferrugineum (L.) Populations (Subalpine Level, Northwestern Alps, France)

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Abstract

The modifications of humus characteristics as a result of the establishment and the increasing cover of *Rhododendron ferrugineum* L. (Ericaceae) in a subalpine meadow were studied in three sites in the northwestern French Alps corresponding to a west–east transect between wet and dry Alps ("Chaîne de Belledonne," "Massif du Taillefer," "Briançonnais"). The physical and chemical parameters of humus and biological parameters were studied during the successive studies.

As opposed to other Ericaceae heathlands on siliceous soils (*Vaccinium* sp., *Erica* sp., *Calluna vulgaris*), with an increasing *Rhododendron* cover, the humus structure changed while some other parameters remain stable or increased. The development of *Rhododendron* populations on calcareous soils (Briançonnais) with maintenance of a calcareous humus has never been checked before.

The modifications of the *Rhododendron* environment under its canopy led to an improvement in its growth conditions (positive feedback).

Introduction

The study of vegetation dynamics concerns changes in species composition, vegetation physiognomy, and the physical environment of the plants. Individuals or populations can often compete with neighboring individuals or populations in two forms (Miles, 1979): a first form where the more successful species use environmental ressources (light, water, nutrients, etc.) at the expense of the lesser competitive ones. In a second form plants frequently modify their own environment and consequently the environment of neighboring species. These ideas are well known, and numerous data have allowed the formulation of a theoretical plant succession pattern (Lepart and Escarre, 1983). Many studies have shown how plants could affect environmental conditions, particularly soil functioning (Vinton and Burke, 1995; Hobbie, 1995; Northup, 1995; Bever, 1994; Gross et al., 1995; Ozinga et al., 1997; Lechowicz and Bell, 1991). Humus form, nitrogen and carbon content, microbial activity, soil pH, and cation exchange capacity are parameters subjected to changes induced by vegetation (Miles, 1985; Richter et al., 1994; Vinton and Burke, 1995; Tian et al., 1997; Groten and Bruelheide, 1997; Saetre, 1998; Watkinson, 1998). Moreover, the more a plant species concentrates biomass and nutrients under its canopy, the longer it will persist on a site and the greater its effect on the environment (Richter et al., 1994; Vinton and Burke, 1995). Hovever, very few studies mention how a given species improves its environment for its own advantage and not only by means of directly inhibiting other species (Berendse, 1994; Bever, 1994; Bever et al., 1997; Van der Puten, 1997; Wilson and Agnew, 1992).

Ericaceous shrubs are known to generate weakly structured humus which can reduce the biological activity of soil (Duchaufour, 1977; Bonneau, 1980; Pornon and Doche, 1995). Ericaceous leaves contain phenolic compounds which make phenol-protein complexes that are very resistant and able to reduce or stop nitrogen mineralization (Handley, 1961, *in* Boullard, 1964; Schvartz, 1975; Haynes and Goh, 1978). These phenolic counpounds can also inhibit mycorrhizal fungi growth and decrease tree germination and seedling growth in species such as *Picea abies* (Pellissier, 1994).

Ericaceous shrubs are able to monopolize space and to structure stable plant communities with homogeneous physiognomy on barren, acidophilous, and unfertile grasslands. Gilot (1967) and Richard and Pautou (1982) also mention the presence of *Rhododendron ferrugineum* on thick, brown, leached soils on calcareous bedrock, following an old decarbonation process.

These closed heathlands have biotic and mechanical resistance to colonization by trees. The maintenance of this resistance depends on the life span of individuals, on their potential for sexual and/or asexual reproduction, and on the demographic structure of their populations (Gimingham, 1972, 1978; Clement and Touffet, 1976; Miles, 1981; Prentice et al., 1987; Doche et al., 1997). For example, the evolution of *Calluna* heathland can be cyclic (Barclay-Estrup and Gimingham, 1969), gradual (Doche, 1990), or regressive (Coquillard and Gueugnot, 1991).

In this study, physical, chemical, and biological properties of humus were studied along with a secondary successional gradient in two acidophilous and one calcareous meadow of *R. ferrugineum* (Ericaceae) heathlands on three sites in the northwestern Alps (1600–2200 m). The main objectives of the study were to determine which changes in humus quality could be induced by *R. ferrugineum* shrubs and if *R. ferrugineum* heathlands have similar detrimental consequences on humus quality at low and high altitudes.

Studied Species and Study Sites

Rhododendron ferrugineum L. is an ericaceous evergreen shrub, reaching a height of 70–80 cm. *R. ferrugineum* forms large heathlands on the north- and northwest-facing slopes at a subalpine level (1600–2100 m) in the French Alps. This species can constitute dense populations with almost 100% of cover, and a single genotype can occupy a large surface and sometimes form a dense patch, suggesting that this species adopts a phalanx growth form (Lovett Doust, 1981; Pornon et al., 1997) with limited intermingling of some genets (Escaravage et al., 1998). A clone about 300 years old (7 m in slope direction) has been investigated using molecular biology techniques (Escaravage et al., 1998).
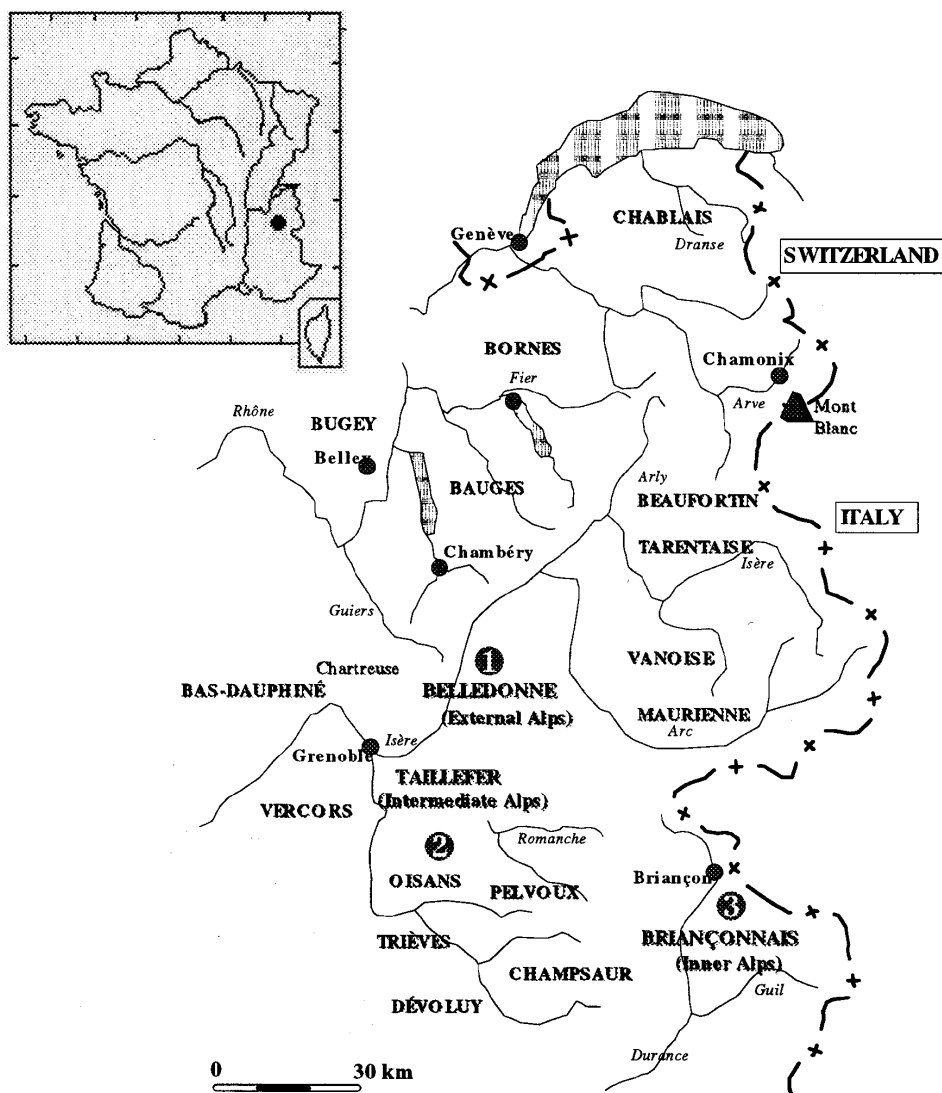
FIGURE 1. The study sites in the northwestern Alps: (1) "Belledonne" (external Alps), (2) "Taillefer" (intermediate Alps), (3) "Briançonnais" (inner Alps).

Along a successional sequence (meadow → open heathland → closed heathland), *R. ferrugineum* shows complementary reproductive strategies. Sexual reproduction decreases and vegetative reproduction increases. The direction toward which the clones extend is mainly determined by the topography (slopes) rather than by the need to escape unsafe sites or to reach new resources. In closed heathland (cover of 90–95%), vegetative reproduction only is maintained (Pornon et al., 1997).

Three study sites were selected in the northwestern French Alps (Fig. 1): the "Chaîne de Belledonne" (45°25′N, 6°10′E), the "Massif du Taillefer" (45°4′N, 5°58′E), and the "Briançonnais" (44°50′N, 6°50′E). A west–east transect went from wet Alps (Belledonne), favorable to *Rhododendron*, to dry Alps (Briançonnais), where shrub potential is reduced whatever the source rock type is. In the inner Alps (Briançonnais), the most dispersed *Rhododendron* heathlands grow over calcareous rocks and siliceous rocks; the *Rhododendron* patches (5–10 m²) do not seem to be able to monopolize meadow areas. In the external (Belledonne) and intermediate Alps (Taillefer), the closed heathlands extend over several hectares in north-facing slopes (Richard and Pautou, 1982; Ozenda, 1981, 1985), although a *Rhododendron* population, which does not compete with other offensive woody species (shrubs, trees), needs 150 years to extend over a meadow area and to occupy 80–90% of space (Pornon, 1994).

The environmental features of each site are summarized in Table 1.

Methods

STRUCTURAL AND BIOLOGICAL RHODODENDRON *CHARACTERISTICS*

In each site (Belledonne, Taillefer, Briançonnais), a succession of three physiognomic stages was studied: a *Nardus stricta* meadow (*Rhododendron* cover: 0–5%), an open *Rhododendron* heathland (cover: 30–40%), and a closed *Rhododendron* heathland (80–96%). In each site, these three stages were 100 m apart. In this study, a synchronous approach was used (different physionomic stages were compared on the same date) because of the slow extension rates of heathlands.

At each site, the *Rhododendron* biomass was measured by random choice (cut and weighing 5 × 1 m² plots at Belledonne, Taillefer) or estimation (individual number × mean height at Briançonnais). The heathland heights and covers were quantified at all sites. The colonization rates were estimated by determining the different age groups in *Rhododendron* populations; the age of each ramet was determined by counting growth rings after cutting the biggest stem (Belledonne, Taillefer). At Briançonnais, the age of the biggest stems found above each soil pit was analyzed in order to determine the influence periods of *Rhododendron* on the humus (structure, physical and chemical characteristics).

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TABLE 1

Ecological features of the three sites.

Massifs:	Belledonne	Taillefer	Briançonnais
Location	45°25′N, 6°10′E	45°4′N, 5°58′E	44°50′N, 6°50′E
Position in Alps	External Alps	Intermediate Alps	Inner Alps
Altitude (m)	1700	1900	2100
Level	subalpine	subalpine	subalpine
Exposition	northeast	northwest	northwest
Precipitation (mm a^{-1})	1800	1800	1400–1600
Snow cover	5–6 months (December to May)		
Source rock	sericitoschist, chlorite schist	amphibolites, gneiss gabbro	calcschist
Mean slope (%)	55	45	45
Forest climax	spruce forest (*Picea abies*)	Spruce forest with *Pinus uncinata*, *P. cembro*	Larch forest (*Larix europaea*)

PHYSICAL AND CHEMICAL ANALYSIS OF HUMUS

Three soil profiles per physiognomic stage and per site were visually described to define the soil types. A set of 10 samples was carried out for analysis at deep horizons, under the meadows, in order to define the precise soil type of each site.

Three humus samples per physiognomic stage at each site were taken in the A1 horizon (0–10 cm; 27 samples total). In the open and closed heathland, soil pits were dug beneath *Rhododendron* crowns and just beside the oldest stems; in the meadow, the humus and deeper horizons were sampled under grass cover.

The chemical parameters of humus (pH, C/N, S/[capillary electrochromatography (CEC)], ions, etc.) were studied for each sample after air drying and sifting (2-mm guage). The analyses were carried out on fine-textured soil using a Carlo Erba NA 1500 for total carbon and total nitrogen, a Tacussel pHN81 pH meter for H_2O and KCl pH, and the hexaminecobalt trichloride method for CEC and metallic cations (AFNOR, 1985).

THIN SECTIONS OF HUMUS

Three thin sections of soil per physiognomic stage and per site (3×3 per site) in the A1 horizon were used in order to study the humus structure. A humus block was collected from each soil pit using metallic boxes with dimensions of $5 \times 5 \times 10$ cm^3 (Kubiena, 1953). The soil samples were then stored at 5°C until sent to the Soil Sciences Laboratory of the I.N.R.A. (Rennes, France) where the thin sections were prepared.

The 27 thin sections were first visually observed by depth levels (0–2 cm; 2–10 cm) and after with a standard microscope ($\times 60$ to $\times 250$). The standardized observations of descriptive forms (different scales were defined before observations) were separately duplicated. Humus structure, aggregation degree, aggregate size, porosity types (cracks, chenals (canals), vesicles, cavities), root density, and stoniness were studied. The thin sections were then analyzed using a Karl Zeiss Jena microscope ($\times 250$ to $\times 630$, natural and polarized light) in order to distinguish organic and mineral matter, and microarthropoda feces. The structure of sections was compared per level and the frequency, size, shape, colour, distribution pattern, and content of aggregates were recorded.

Porosity was quantified using Optimas image analyser software; for each thin section, 40–45 windows (8.5 × 6.5 mm = 55.25 mm^2 per window, about 22–25 cm^2 per section) were analyzed per depth level (0–3; 3–6; 6–9 cm) on the entire section.

The excrement pedofeatures were identified (intact and ageing excrements) using the *Handbook for Soil Thin Section Description* (Fedoroff et al., 1985).

HUMUS MICROFAUNA ANALYSIS

Three humus samples per physiognomic stage (meadow, open and closed heathland) from each site (Belledonne, Taillefer, Briançonnais) were taken in the litter layer and in the A1 with a bulb dibber (300 cm^3 per sample, about 1200 cm^3 per physiognomic stage and per site).

The sampling was carried out after one week of fine weather. The sampling dates and the soil and air temperatures for each site are as following: Belledonne (29 June 1998; mean soil temperature in A1, under meadow, open and closed heathland: 16°C, 13°C, and 11.8°C, respectively; air temperature during the sampling : 20.5°C), Taillefer (1 July 1998; soil: 16.2°C, 14°C, and 12.5°C; air: 22°C), and Briançonnais (9 July 1998; soil: 9.9°C, 7.9°C, and 6.3°C; air: 14°C).

The microfauna extraction was carried out using a Berlese apparatus (Vannier, 1970). In the laboratory, each humus volume

TABLE 2

Structural and biological characteristics of each physiognomic stage in the three sites. M = meadow, O.H. = open heathland, C.H. = closed heathland.

Sites:	Belledonne			Taillefer			Briançonnais		
Physiognomic stage:	M	O.H.	C.H.	M	O.H.	C.H.	M	O.H.	C.H.
Mean height of *Rhododendron* (cm)	22	40	62	—	42	70	—	20	40
Rhododendron cover (%)*	1%	28%	52%	—	16%	96%	—	10–15 %	30%
Rhododendron biomass (t DW ha^{-1})	<0.1	16	31	—	8 to 9	64	—	3 to 4	10 to 13
Dominating age groups**	50	100	120–150	—	100	150–300	20–40	40–60	60–90
Vegetation physiognomy	Scattered shrubs	Mosaic of meadow and heathland	Dense heathland	Scattered shrubs	Mosaic of meadow and heathland	Very dense heathland	Scattered shrubs	Mosaic of meadow and heathland	Mosaic of meadow and heathland (40–50%)
Co-dominating species (cover: 30–60%)	*Nardus stricta*	*N. stricta, Vaccinium myrtillus*	*Vaccinium myrtillus, D. flexuosa*	*Nardus stricta*	*V. myrtillus, D. flexuosa*	*Vaccinium myrtillus*	*N. stricta, Sesleria caerulea*	*N. stricta, Sesleria caerulea*	Under-shrubs: *V. myrtillus*, herbaceous spp. (10–20%)

* Specific frequence (assimilated to the cover; Gounot, 1969) measured by linear assessment (minimum 100 points spaced out at 40 cm each).

** In "Belledonne" and "Taillefer" (Pornon, 1994). Age of biggest stems in "Briançonnais."

TABLE 3

The chemical parameters of humus and meadow soils in each physiognomic stage in the three sites. Mean values (± standard deviation) of 3 samples in humus (0–10 cm). M = meadow, O.H. = open heathland, C.H. = closed heathland.

Depth: 0–10 cm	C (%)	N (%)	C/N	Absorption complex (meq./100g) to soil pH						Al/Ca*	S	CEC	S/CEC	pH	
				Ca^{2+}	Mg^{2+}	K^+	Na+	Fe^{2+}	Al^{3+}					H_2O	KCl
Belledonne															
M	11.18 ± 1.72	0.85 ± 0.13	13.15 ± 0.01	1.63 ± 0.63	0.70 ± 0.12	0.22 ± 0.06	0.13 ± 0.13	0.02 ± 0.01	0.69 ± 0.41	0.42	2.68 ± 0.9	10.24 ± 1.35	26%	4.6 ± 0.11	3.6 ± 0.13
O.H.	13.23 ± 3.63	0.79 ± 0.12	16.43 ± 2.12	2.29 ± 0.80	0.81 ± 0.11	0.21 ± 0.03	0.04 ± 0.02	0.06 ± 0.05	1.06 ± 0.33	0.46	3.35 ± 0.9	12.16 ± 5.76	27%	4.4 ± 0.14	3.5 ± 0.60
C.H.	10.23 ± 0.90	0.61 ± 0.07	16.77 ± 0.59	1.80 ± 0.87	0.80 ± 0.35	0.24 ± 0.01	0.09 ± 0.01	0.06 ± 0.04	1.18 ± 0.35	0.66	2.93 ± 1.1	8.13 ± 3.3	36%	4.4 ± 0.14	3.3 ± 0.19
Taillefer															
M	12.67 ± 2.00	1.04 ± 0.16	12.18 ± 0.02	1.61 ± 0.41	0.70 ± 0.24	0.24 ± 0.07	0.09 ± 0.07	0.01 ± 0.00	1.68 ± 0.18	1.04	2.65 ± 0.6	8.95 ± 2.72	29%	5.2 ± 0.23	4.1
O.H.	14.6 ± 3.48	0.91 ± 0.20	16.04 ± 0.94	3.04 ± 1.09	0.86 ± 0.44	0.25 ± 0.03	0.08 ± 0.02	0.02 ± 0.02	1.76 ± 0.21	0.58	4.23 ± 1.5	17.09 ± 2.64	25%	5 ± 0.21	4
C.H.	15.75 ± 1.70	0.94 ± 0.12	16.75 ± 1.03	5.51 ± 1.17	1.47 ± 0.28	0.33 ± 0.02	0.09 ± 0.05	0.02 ± 0.02	0.98 ± 0.16	0.18	7.40 ± 1.5	12.14 ± 3.39	61%	5.1 ± 0.18	3.8
Briançonnais															
M	9.84 ± 3.37	0.69 ± 0.21	14.26 ± 0.71	18.21 ± 5.8	1.9 ± 0.74	0.37 ± 0.11	0.11 ± 0.11	0.01 ± 0.00	0.11 ± 0.10	0.00	20.59 ± 6.45	20.49 ± 5.44	100%	7.1 ± 0.13	5.6 ± 0.49
O.H.	13.1 ± 2.46	0.82 ± 0.09	15.97 ± 1.33	20.6 ± 3.8	2.22 ± 0.58	0.33 ± 0.14	0.16 ± 0.10	0.01 ± 0.00	0.07 ± 0.06	0.00	23.31 ± 4.09	25.94 ± 3.74	90%	7.4 ± 0.16	6.3 ± 0.17
C.H.	13.24 ± 2.13	0.79 ± 0.10	16.76 ± 0.51	28.49 ± 5.2	1.69 ± 0.71	0.36 ± 0.10	0.16 ± 0.09	0.01 ± 0.00	0.04 ± 0.03	0.00	30.70 ± 5.81	28.86 ± 0.70	100%	6.9 ± 0.33	5.7 ± 0.23

* Ratio to define the humus types (Duchaufour, 1989).

TABLE 4

The main soil types in each site (Baize and Girard, 1992; italics, C.P.C.S. classification, 1967).

Belledonne	Taillefer	Briançonnais
Acid brown soils (brunisols oligo-saturés) to *ochre podzolic soils* (podzosols ocritiques)	*Acid brown soils to modal brown soils* (brunisols oligo- à mésosaturés)	*Calcareous brown soils* (calcosols)

(300 cm^3) was put in a funnel surmounted by a 50 watt light bulb for 10 days. The microfauna migrated by negative phototropism but also by decreasing humus humidity and increasing humus temperature. The microfauna samples were collected in alcohol (70°) in test tubes.

Each microfauna sample was identified for taxons and classification according to diet (Pesson, 1971; Bachelier, 1978). Some indices and ratios were calculated (Simpson diversity, Soerensen similarity, Acariens/Collemboles) to compare the biological activities of humus between the sites and under the different physiognomic stages at each site.

Results

The structural and biological characteristics of each physiognomic stage are summarized in Table 2. These results confirmed our fields observations and the sparse literature data on the colonization potentialities of *Rhododendron ferrugineum*; the shrub characteristics and the dynamics of *Rhododendron* heathlands were very different in inner Alps as compared to intermediate and external Alps, where their potential is optimal.

PHYSICAL AND CHEMICAL ANALYSIS

The chemical parameters of humus and the main soil types under meadow of each site are presented, respectively, in Tables 3 and 4 (chemical and physical parameters of depth horizons are not presented).

The ANOVA test allowed us to indicate the significant effects ("site," "vegetation type") for each variable studied in the humus. The Duncan's multiple comparison of means allowed us to pool the "site" and "vegetation type" data for each variable (Tables 5 and 6).

There was an important "site" effect for 12 variables (86%) and also an important "vegetation type" effect for 10 variables (71%) out of 14. The three sites were not individualized (83%, 75%, and 75% of variables have at least one "site" effect, respectively, for Belledonne, Taillefer, and Briançonnais), but the vegetation types were well individualized (meadow, 70%, and open and closed heathlands, 40% and 30%, respectively). Because of an increasing influence of *Rhododendron*, there was a proximity (50%) between open and closed heathlands (Table 5). The correlation numbers between vegetation types for all the studied variables (Table 6) indicated that in Belledonne, the meadow was a differentiated type.

At the three sites, the humus pH was not modified by the *Rhododendron* colonization (open heathland) even when the pH values were near neutrality (calcosols in inner Alps). Under the influence of *Rhododendron* (closed heathland), the pH stability has been maintained for the past 150 to 300 years on siliceous rocks and for the past 60–90 years on calcareous rocks.

At two sites (Taillefer and Briançonnais), the carbon rates (and organic matter) in humus increased slightly with *Rhododendron* colonization (open heathland) and stabilized with increasing influence of the shrubs (closed heathland). In Belledonne, this evolution was not significant; the bioturbation was probably more important.

The sum of exchangeable bases in humus (S = Ca^{2+} + Mg^{2+} + K^+ + Na^+) increased with space monopolization by *Rhododendron*

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TABLE 5

"Site" and "vegetation type" effects for 14 physical and chemical variables (ANOVA, Duncan grouping). Site (B = Belledonne, T = Taillefer, Br = Briançonnais) and type (M = meadow, O.H. = open heathland, C.H. = closed heathland). Shaded boxes have a significant effect.

Variables	"Site" effects						"Vegetation type" effects						Effect (p<0.05)	
	B	T	Br	B-T	B-Br	T-Br	M	OH	CH	M-OH	M-CH	OH-CH	SITE	TYPE
C (%)										■		■		■
N (%)		■			■								■	
C/N							■					■		■
Ca²⁺	■	■	■				■	■	■				■	■
Mg²⁺	■	■	■				■						■	
K⁺	■	■	■							■	■	■	■	■
Mn²⁺	■	■	■										■	
S(Ca,Mg,K,Mn)	■	■					■		■				■	
CEC	■	■					■					■	■	
S/CEC	■	■					■	■	■				■	
Fe³⁺	■	■					■					■	■	
Al³⁺	■	■	■					■			■		■	
Na²⁺			■	■									■	
Porosity	■					■	■					■	■	■
Effects total	10	9	9	1	1	1	7	4	3	2	2	5	12	10
Percentage*	83	75	75	8	8	8	70	40	30	20	20	50	86	71

* Calculated only with variables having at least one effect.

populations, except at Belledonne, where this evolution was dependant on the Ca^{2+} increase, and at Taillefer, where the increase was secondarily dependant on the Mg^{2+} increase. At the three sites, the saturation index (S/CEC) did not evolve with *Rhododendron* colonization but increased during the heathland aging when the cover and the biomass were high. The humus types defined under each physiognomic stage at the three sites are presented in Table 7.

THIN SECTIONS OF HUMUS

At the three sites and under each physiognomic stage, granular and crumbly structures characterized the humus between 2 and 10 cm of depth. During the *Rhododendron* colonization, a tendency to improve degree of aggregation (macroaggregation at Belledonne, microaggregation at Taillefer, stability at Briançonnais) was estimated by standardized observations (Table 8). The root densities tended to decrease with *Rhododendron* colonization at the three sites and the humus stoniness was very high (27%) under closed heathland at Taillefer.

The thin sections under the meadow (Belledonne, Briançonnais) showed high frequencies of fine pedofeatures, most of them produced by oribates and enchytraeids, whereas the structure under closed heathland was essentially made up by earthworm excrements (>2 mm, irregular shapes with mixed mineral and organic elements). The structure of the open heathland section was intermediate, but closer (more compact) under the grassland than under the closed heathland sections.

The mean porosity of meadow humus was higher at Taillefer (35%) and Briançonnais (30%) than at Belledonne (15%). Under the

increasing influence of shrubs, the porosity of humus increased at the three sites from meadow to open heathland, mainly at Belledonne (Fig. 2). In this same site, the porosity evolution continued distinctly until closed heathland (same evolution at Briançonnais). The changes at Taillefer were less important because the humus porosity of meadows was already high; with shrubs, it increased from 15% to 25% and seemed to stabilize during the heathland aging (around 40%); in this site, the *Rhododendron* populations in closed heathland had also a long-term influence on humus (past 150 to 300 years) and the heathland structure was different from other closed heathlands (Table 2).

HUMUS MICROFAUNA ANALYSIS

Except at the Taillefer site, the number of individuals increased during the colonization and monopolization of meadows by *Rhododendron* populations (Table 9). This increment was dependant on plant biomass augmentation (abundant litter).

At the Taillefer site, the open and closed heathlands were characterized by very low quantities of microfauna organisms. In closed heathland, *Rhododendron* influence of humus evolution was very long (150–300 years) and important (biomass: 64 t DW/hectare; cover: 96% [1195 ± 427 shoots/m²]; Pornon et al., 1997). In open heathland, the cover of each *Rhododendron* shrub was more dense (1588 ± 469 shoots/m²) than in the two other sites (1333 ± 348 shoots/m² in Belledonne, lower 900–1000 shoots/m² at Briançonnais). The microclimatic conditions in shrubs could explain these low results.

At the three sites, the taxon Oribatulidae (Acarida, Oribatida) was the most abundant (40%–60% at Belledonne and Taillefer, 20%–30%

TABLE 6

Correlation number between "vegetation type" and "site" for 14 physical and chemical variables (Duncan grouping). M = meadow, O.H. = open heathland, C.H. = closed heathland.

"Veg. type" effects	M	O.H.	C.H.	M-O.H.	M-C.H.	O.H.-C.H.
Belledonne	4*	1	1	1	2	7
Taillefer	5	6	7	3	3	2
Briançonnais	2	2	3	3	2	3

* In Belledonne, four variables have a significant meadow effect.

TABLE 7

The humus types under every physiognomic stage in the three sites (Duchaufour, 1997; italics, Baize and Girard, 1992).

	Belledonne	Taillefer	Briançonnais
Meadow	oligotrophic (acid) mull; tendency mull-moder	mesotrophic mull to	calcareous mull (*dysmull*)
Open heathland	mull-moder	oligotrophic mull	calcic mull
Closed heathland	oligotrophic mull	mesotrophic mull (*amphimull*)	calcareous mull (*dysmull*)

TABLE 8

Micromorphologic characterization of 27 thin sections of humus using standardized methods (9 per site). In each column, the results (aggregate size, structure, aggregation degree, porosity, etc.) represent the analysis of 3 thin sections by humus (about 120–140 cm²) and by physiognomic stage. M = meadow, O.H. = open heathland, C.H. = closed heathland.

Site:	Belledonne						Taillefer						Briançonnais					
Depth:	0–2 cm			2–10 cm			0–2 cm			2–10 cm			0–2 cm			2–10 cm		
Physiognomic stage:	M	O.H.	C.H.	M	O.H.	C.H.	M	O.H.	C.H.	M	O.H.	C.H.	M	O.H.	C.H.	M	O.H.	C.H.
Aggregates size* (M → O.H. → C.H.)																		
<2 mm	4	4	4	3	2	1	5	4	4	3	4	4	5	4	5	3	1	2
2–5 mm	2	2	1	2	3	1		1	2		1	2	1	2	1	3	3	3
Macro-aggregates				1	2	4										1	2	2
Structure (X: tendencies)																		
None							X	X					X	X				
Granular	X	X	X	X			X	X	X	X	X	X	X	(X)	X	(X)	(X)	X
Crumbly			X	X	X	X			X		X	X				X	X	X
Aggregation degree																		
Important	X	X	X			X	X	X	X	X	X	X	X	X	X		X	X
Intermediate					X					X	X	X				X		(X)
Weak				X	X													
Porosity types** (E: intEr-aggregate, A: intrA-aggregate)																		
With cracks	■	■	■	E	E	E	■	■	■	A E	A		■	■	■	A E	A	A
With chenals (channels)	■	■	■			A	■	■	■	A			■	■	■	A	E	E
With vesicles	■	■	■		A	A	■	■	■	A		A	■	■	■		A	
With cavities	■	■	■	A	E	E	■	■	■	E	E	E	■	■	■	A E	E	E
Root density (/cm2)																		
Living roots	1.1			3.3	2.3	2.9	1.1			5	4.5	3.1	20			7	1.5	4
Dead roots	1.15			4.5	3.4	5.1	0.9			13	8.5	2.5	3			10	6	8.8
Root diameters ≤ 2 mm						0.02				0.01								0.06
Stoniness (% / thin section); depth: 0–10 cm																		
under 2 mm	■	■	■	1.3	0.5	0.8	■	■	■	0.11	0.5	1.1	■	■	■	0.3	0.2	0.6
2 to 20 mm	■	■	■	17.7	5.7	4.4	■	■	■	0.5	11.5	26	■	■	■	0	0.9	1.2
Total	■	■	■	19	6.2	5.2	■	■	■	0.61	12	27.1	■	■	■	0.3	1.1	1.8

* Aggregate size: (scale 1 to 5; estimation of relative abundance); 1: <5%; 2: 5–25%; 3: 25–50%; 4: 50–75%; 5: >75%.

** Porosity types (Baize and Jabiol, 1995).

at Briançonnais). These proportions tended to increase in open and closed heathlands. The taxon Nematocera (Diptera) reached 10%–26% at Briançonnais but only 0%–6% at the other two sites. The taxon *Collembola arthropleona* represented a 2–7% increase in closed heathland (9%, 13%, and 23%) at the three sites. Those taxa constituted the micro- and macro-phytophagous organisms.

In humus of the meadows and closed heathlands, 78% to 88% of organisms were phytophagous and 10% to 21% were carnivorous; the percentages were less important for phytophagous organisms (63% to 74%) and more important for carnivorous animals (22% to 37%) in open heathlands humus. In all sites and physiognomic stages, the percentage of organisms with other trophic diets (omnivorous, saprophytic) fluctuated between 0 and 8%.

In the closed heathland of the three sites, the ratio Acarida/*Collembola* indicated a defaced biocoenosis, a simplification and an imbalanced ecosystem as compared with a climax ecosystem (Bachelier, 1978). The similarity between meadows of the three sites was always very constant (comparison of two biotopes with Soerensen index: >84%); it decreased in closed heathlands principally between Belledonne/Taillefer (48%) and Belledonne/Briançonnais (52%). At the same site, the index was always >69% in Belledonne and Briançonnais stages, and it varied between 40% and 62% in Taillefer stages. The Simpson index decreased with colonization and monopolization of meadows by *Rhododendron* populations in Belledonne and

Briançonnais, indicating a decrease of the standing diversity; in Taillefer, the index slightly increased in open and closed heathlands.

Discussion

Mature and degenerate heathlands on siliceous soils in the different elevation levels were associated with a moder or a raw humus (mor) showing limited biological activity (Bernier et al., 1994; Pellissier, 1994; Bernier and Ponge, 1994: *Vaccinium myrtillus*) (Duchaufour, 1977; Bonneau, 1980; Doche, 1986: *Calluna vulgaris*) (Gloaguen et al., 1980: *Erica cinerea, E. ciliaris*) (Aubert, 1976: *Erica arborea, E scoparia*), whereas meadow humus was known to be more active (Duchaufour, 1977; Richard and Pautou, 1982).

Our results showed that the colonization of subalpine meadows by *Rhododendron ferrugineum*, with an increasing cover, could improve the humus structure (porosity principally); this effect was even more obvious at Belledonne where the grassland was pastured and the humus therefore compacted.

At each site, the humus typology showed tendencies to global improvement of A1 horizons (Table 5) even if, in closed heathland, litter layers got thicker (2–5 cm) with accumulation of plant biomass in plant communities. In these ecosystems, the humus functioning remained efficient. Some humus parameters increased (Ca^{++} concen-
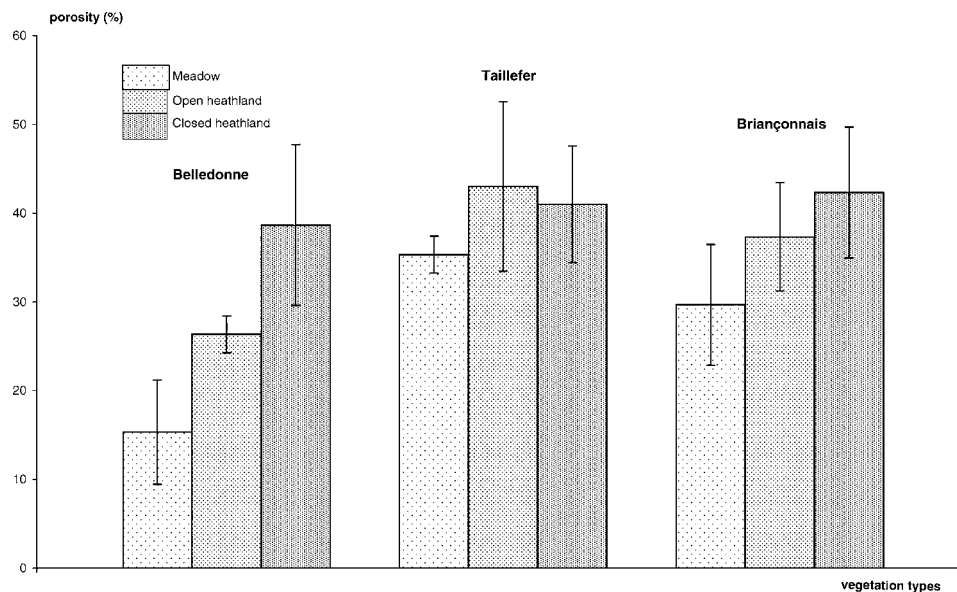
FIGURE 2. Evolution of humus porosity in the three site with an increasing influence of shrubs (meadow to closed heathland).

tration, individual number of microfauna), tended to remain stable (pH), or weakly increased (C/N, S/CEC).

The Ca^{++} accumulation under heathlands resulted in biomass growth and consequently litter growth (nutrients were taken from depth by biological raising); the acidophilous litters supplied the same quantities of Ca^{++} and Mg^{++} as the better litters. Mg^{++} was more labile and did not increase (or increased weakly) during the succession. Ca^{++} was partly stocked in humus in an inassimilable form and released very slowly (Vedy, 1973; Toutain, 1974; Messenger, 1975 *in* Duchaufour, 1977).

The presence and the development of *Rhododendron* populations on calcareous mull with maintenance of the physical and chemical characteristics and improvement of porosity were unknown at Briançonnais.

This global amelioration of humus could be explained at different levels.

(1) Earthworm's role. During our field work, some earthworms were frequently observed under the closed heathlands but for technical reasons, no quantification was realized at the three sites. However, under the closed *Rhododendron* plot (about 3 m²) in the subalpine level of the Northern Alps, 30 worms per m² were counted (Gandoy, 2000), belonging to the genus *Lumbricus*. They could structure the upper layers of the soil (Ponge and Delhaye, 1995; Grossi et al., 1997) and resurface nutriments; their feces were richer in Ca^{++}, Mg^{++}, NO_3^-, P, and K than surrounding soil (Bachelier, 1978). In *Vaccinium* heathlands of the same level in the mountain, there were only 5 worms per m² (Bernier and Ponge, 1994).

(2) The Ca^{++} increase was favorable to the development of the clay humus complex and consequently to the improvement of the humus structure and humus stability (Duchaufour, 1977) (from meadow to closed heathland, tendency from granular to crumbly structure with some macro-aggregates).

(3) The modifications of humus were a direct consequence of the changes in species composition but also in the vegetation structure. At the beginning of the succession, under young *Rhododendron* shrubs isolated in a meadow, some other species took part in humus evolution for 50 to 100 years (*Deschampsia*

flexuosa, *Vaccinium myrtillus* principally). These two species which have good capacities to colonize meadows and to structure a moder and a raw humus (Duchaufour, 1989; André, 1994; Pellissier, 1994; Ponge et al., 1994) were inhibited in their development by *Rhododendron* canopy growth and nutritional competition (concept of "asymmetric competition": Weiner, 1990). In closed heathlands, under the canopy, the vegetal cover and biomass (small shrubs and herbaceous plants) regressed, mainly at Taillefer (cover: 15%; biomass: <1t DW ha⁻¹ with 0.74 t of *Vaccinium* sp.); concurrently, mosses (15%) and a litter layer (cover: 90%; thickness: 4 ± 1.2 cm) developed. At the two other sites, the values evolved in the same direction but under the *Rhododendron* canopy (less closed), the species regression was less important.

(4) The tannin effect was more important in *Vaccinium* litter than in *Rhododendron* litter (tannin equivalent: 230 mg g⁻¹ in *Vaccinium* leaves and only 120 mg g⁻¹ in *Rhododendron* leaves; Gallet and Lebreton, 1994). This tannin effect tended to reduce or to block the nitrogen mineralization (Handley, 1961; Schvartz, 1975 *in* Duchaufour, 1977). The development of *Rhododendron* population in *Vaccinium* communities improved the humus dynamics.

(5) The changes were also induced by modifications of microclimate under isolated *Rhododendron* stands and under the closed *Rhododendron* populations; these modifications were favorable to biological soil activity. The canopy, the stems, and branches of shrubs which had a sheltering effect, reduced desiccation during the summer. Better moisture conditions were characterized by establishment in closed heathland of moisture plants (*Adenostyles alliariae* at Belledonne and Taillefer) and mosses; these conditions were favorable to *Rhododendron*, which had high water needs (Landolt, 1977; Richard and Pautou, 1982; Pornon, 1994). Under *Rhododendron* closed heathlands, during vegetative period (May to September), the humus temperatures were 2.5°C to 4°C below temperatures of meadows humus (Pornon and Doche, 1995; Pierre, 1996). The effect of plant cover on humus temperatures was variable and the latter in turn had variable effects on phenology, plant growth, and more precisely root growth (Bannan and Bode *in* Tranquillini, 1979),

TABLE 9

Evolution and comparison of microfauna in humus under each physiognomic stage in the three sites (3 × 300 cm³ are analyzed per stage). M = meadow, O.H. = open heathland, C.H. = closed heathland.

Sites	Belledonne			Taillefer			Briançonnais		
Physiognomic stage	M	O.H.	C.H.	M	O.H.	C.H.	M	O.H.	C.H.
Oligochete	2	1	2	4	3	—	46	—	7
Arachnida	—	—	2	6	—	—	—	1	1
Myriapode Chilopoda	—	2	—	2	—	—	—	—	—
Acarida									
Gamasida	17	57	69	62	5	2	53	182	88
Oribatida Belbidae	13	11	8	21	6	4	11	4	196
Brachychthoniidae	7	4	32	47	—	1	23	1	47
Camisia	10	—	67	15	—	—	2	1	15
Oripodidae	78	208	849	174	15	9	146	216	505
Pelopidae	2	4	—	3	—	—	5	5	—
Galumnidae	4	—	16	—	—	—	—	—	6
Phthiracaridae	1	9	15	8	1	1	2	17	88
Prostigmata	3	36	89	12	7	—	42	55	87
Astigmata	2	4	10	1	—	—	2	5	2
Apterygota									
Collembola: Protura	—	1	—	—	—	—	5	6	—
Diplura	—	2	—	—	—	—	—	—	—
Arthropleona	4	11	174	16	1	2	43	57	372
Symphypleona	—	4	1	—	—	—	—	1	—
Pterygotes									
Diptera: Nematocera	11	30	28	25	—	1	178	156	166
Brachycera	5	13	—	1	—	—	2	21	—
Larva	1	6	3	1	—	—	5	1	2
Homoptera auchenorrhynque	3	16	2	2	—	—	31	14	25
stenorrhynque	—	1	—	—	—	—	33	2	2
Coleoptera	5	12	1	2	—	—	14	25	7
Staphylinidae	6	5	—	3	—	—	4	1	4
Phytophagous larva	—	5	—	1	—	—	—	3	—
Carnivorous larva	2	4	2	—	3	—	1	6	—
Hymenoptera	7	27	2	4	—	—	19	22	10
Heteroptera	2	3	1	—	—	—	—	—	2
Orthoptera	—	1	—	—	—	—	—	—	—
Thysanoptera	2	2	—	—	—	1	7	8	4
Psocoptera	1	2	1	2	—	—	2	26	—
Anoplura	—	—	—	—	—	—	—	—	3
Lepidoptera larvae	—	—	—	—	—	—	—	—	4
Total (3 × 300 cm³ = 900 cm³)	188	481	1374	412	41	21	676	836	1643
Mean for 300 cm³	63	160	458	137	14	7	225	279	548
Standard Deviation	±24	±37	±124	± 7	± 8	± 2	±81	±131	±151
Acarid	137	333	1155	343	34	17	286	486	1034
Collembola	4	18	175	16	1	2	48	64	372
Acarida/Collembola*	**34**	**18**	**7**	**21**	**34**	**8**	**6**	**8**	**3**
Taxon number	23	28	21	22	8	8	23	25	23
Common taxons to 3 stages/site		17			5			17	
M-OH; OH-CH; M-CH**	82%	69%	86%	47%	62%	40%	92%	75%	78%
Meadows comparisons**		Bell./Taill.: 84%			Bell./Brian: 91%			Taill./Brian: 84%	
Closed heathland comparisons**		Bell./Taill.: 48%			Bell./Brian: 52%			Taill./Brian: 82%	
Standing diversity in each stage***	5.1	4.6	2.4	4.5	5.2	4.9	7.1	6.2	5.6

* This ratio characterizes the evolution level of the ecosystem; it decreases with simplification and weak stability of the ecosystem.

** Soerensen index (1948). Similarity quotient between 2 stages. 2c/(a+b) × 100. 0% = no similarity; 100% = total similarity. (a) = species number in stage A, (b) = species number in stage B, (c) = number of common species in stages A and B.

*** Simpson index (1949); $N(N-1)/\sum n(n-1)$. The standing diversity increases with the index increase. (N) = individuals number in the stand, (n) = individual number of each species or taxon.

nutrient absorption (Blackman, 1936; Dadykin, 1958), pedological processes as mineralization (Bonneau, 1980; Roze, 1986; Tavant, 1986), and on microbiological activity.

Lower mineral nitrogen amounts were observed in closed heathland with lower soil temperatures (Pornon and Doche, 1995). The variations of different mineral nitrogen forms could be important in the long term because the ability of plants to absorb NH_4^+ or NO_3^- and the stability of these ions were different. Woody plants, as the Ericaceae, are likely to absorb NH_4^+ (Boxam and Roelofs, 1988;

Scheromm and Plassard, 1988; Hoffmann, 1966; Hoffmann and Fiedler, 1966), while herbaceous are not (Hull and Muller, 1977; Jenny et al., 1950; Salsac et al., 1987) except *Deschampsia flexuosa* and *Nardus stricta* (Le Tacon et al., 1982; Troelstra et al., 1995). With ericoïd mycorrhizal roots, ericaceous shrubs used organic nitrogen forms in the humus (Read, 1983, 1991, 1996) and consequently the heathland shrubs were more competitive for nitrogen nutrition than meadow plants. At Taillefer, the growth of current-year twigs was also high in closed populations (Pornon et al., 1997) where senescence patches were not observed. Pornon et al. (2000) mentioned that the range of genetic diversity diminished from the open to the closed populations; there was a selection of the most competitive genotypes (high growth) in old closed heathlands.

All the changes in the environment under *Rhododendron* canopy are induced by its own development and lead to an improvement in growth conditions (Pornon et al., 1996). This process in which a population (or a community) modifies the environment, making it more suitable for this population (or community) is connected with the concept of "positive-feedback switches". Wilson and Agnew (1992) defined four types of switches in accordance with the community's number and with the changes of an environmental factor "in" and "out" of the patches generated by each community ("one-sided" and "external reaction" switches with one community; "symmetric" and "two-factors" switches with two communities). The *Rhododendron* population induces changes in the environment, in patches where it is present and the boundaries cannot be stable because populations can invade the unmodified environment (one-sided switch). The *Rhododendron* shrub maintains (pH) or improves (porosity principally) some parameters of humus but it is also the structure of closed heathland (news microclimatic conditions), which explains the "positive-feedback switch". The consequences of the ability of plants to influence soil processes remain unexplored and therefore the plant-soil feedbacks are still unrecognized (Bever, 1994; Van Der Putten, 1997). The ability of *Rhododendron* to absorb NH_4^+, the only nitrogen form available below a certain threshold of low temperatures, its ability to modify its reproduction strategy (Pornon et al., 1997), the growth of current-year twigs highest in closed population and the absence of senescence patches are indicators of a positive-feedback mechanism. The humus conditions resulting from *Rhododendron* dynamics allow species that have changed the humus to remain, to monopolize solely by layering the space from 60 to 80 cm in depth. Normally, the effects of plants on soil results in a beneficial future for generations of the same species (Van Der Putten, 1997) and conversely to *Rhododendron* populations which do not have offspring under the canopies of closed heathlands. Bever et al. (1997) emphasize that asexual reproduction may be advantageous when genotypes within a population experience a strong positive environmental feedback on fitness.

With all the environmental modifications, the shrub populations compete more efficiently with other species (grasses, dwarf shrubs, trees) and contribute to stop the forest colonization. In the long term, on the north-facing slopes of wet subalpine level (external and intermediate Alps), the closed heathlands are successful in monopolizing large areas; on a human scale, these plant community remain physiognomically stable but their internal evolution must be studied.

Acknowledgments

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