



Heathlands functioning in a perspective of climate warming

Estimation of parameters, elements for discrete event simulation

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Abstract

Three *Calluna vulgaris* (L.) Hull heathlands (1100, 1500 and 1780 m altitude) are studied in order to establish and estimate parameters which will be integrated in a discrete event simulation of heathland functioning in the case of a 2 °C climate warming. The sites, situated in the Chaîne des Puys and the Massif du Sancy (France), present similar conditions for *Calluna* growth: bedrock (trachyt), exposure and slope, so that they can be compared on a climatic basis. Main parameters sampled are: age distributions, life expectancies, layering probabilities, annual growths, biomasses (standing crop), C/N rates and potential respiratory of soils. In addition, experiments were carried out on germination, hypocotyle elongation and growth of mycorrhizal fungi in order to estimate the inhibitory-to-growth action against the substitution process. On one stand (exhibiting gaps) the patch structure of *Calluna* plants was recorded and mapped. The rising of biomass expected is calculated according to the Aerts's model, as a function of nitrogen availability which would increase under a scenario of climate warming. From a similar point of view, layering probabilities, life expectancies and inhibition of seedlings survival modelling – under a linear model assumption – are proposed.

Introduction

This article is one of a series reporting the results obtained on *Calluna* heathlands established on volcanic substrates in the French Massif Central, Silver birch (*Betula pendula*) and Scots pine (*Pinus sylvestris*) settlement and growth (Prévosto et al. 1999a, b) on these heathlands and the results of modelling.

The existing model is an individual-based one using the Discrete Event Simulation method, taking into account the spatial effects and the purpose of the simulations laid mainly in the heathland dynamics versus wood substitution. The model handles the individuals by means of a grid, each cell of which (corresponding to an average diameter of 0.7 m) can be occupied by a single *Calluna* plant or by an herbaceous covering. The neighboring pattern we chose is an hexagonal compact structure in which each cell is surrounded

by 6 others. According to many authors' field observations, adventitious rooting is the main method of reproduction of *Calluna* in the model, and, for a small amount, the production of seeds. The attributes (coordinates, dendrometric characteristics, competition index . . .) of the woody individuals in competition with *Calluna* are stored in a separate layer of memory. Results of simulations concern: (i) demographic aspects of *Calluna* heathlands, Scots Pine and Silver Birch, (ii) dendrometric parameters of trees, and (iii) characteristics of heathlands such as percentage of cover, distribution of ages and biomass. In addition to these statistical results, the geographic repartition of plants and trees can be obtained for each time step of the simulations. Some additional details and technical points of the software can be found in Coquillard (1995) and Coquillard & Hill (1997).

The intention was to introduce in the model the climatic variations forecasted by meteorological modellers due to the greenhouse effect (the average annual temperature would progressively gain 2 °C in 2020 compared to the 1990 value) and to simulate the vegetation change at the tree line level and higher altitudes. Several models were proposed by authors in order to predict vegetation dynamics or vegetation types at mountain and subalpine levels (Brown 1994) or at several scales (Neilson & Mark 1994; White & Running 1994). Mainly based on computation rules and holistic variables (leaf area index, water balance, solar radiation, soil saturation...), no one, to our knowledge, has attempted to predict the vegetation dynamics at medium scale, integrating individual interactions, competition between species, changes in reproduction rates and biomass response to climate modifications.

In this paper, we present the results of sampling and some elements of modelling which will be introduced as input values either as initialization parameters or computation rules parameters. These parameters concern the demographic aspects of *Calluna* (distribution of ages, life expectancy, layering process) and some elements of the nitrogen cycle (annual nitrogen absorption). In addition, to verify the hypothesis of null influence of weak differences between parent materials, we measured the C/N ratio and the potential respiratory index of soils on each site we studied. Although the model does not handle the individual growth of *Calluna*, the variation of average aerial biomass could be inferred from statistical results. Thus, we carried out several measurements in order to estimate the equilibrium biomass at different altitudes.

Lastly, considering that the inhibitory factor to germination from *Calluna* litter reported by numerous authors could be one of the main factors driving the vegetation dynamics of heathlands, particularly the settlement of Scots Pine and Silver Birch (Robinson 1972; Marcelis 1981), we carried out some experiments on germination of 8 species of heathlands, hypocotyle elongation (*Solanum lycopersicum*) and growth of mycorrhizal fungi (7 species), using alcoholic extracts from leaves and supporting tissues of *Calluna* harvested on stands.

According to climate model predictions (Rind et al. 1989) we considered the future variations of precipitation as a non-limiting factor of growth at subalpine level. Assuming the altitude gradient of temperature is equal to 0.5 °C/100 m, field samplings were achieved on three sites at 1100, 1500 and 1780 m alt. respec-

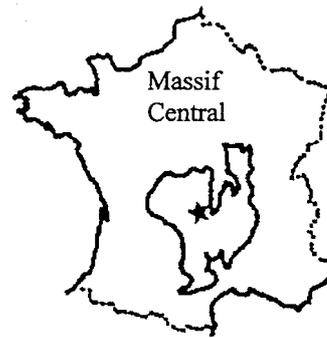


Figure 1. Situation of the stands in the French Massif Central.

tively, in order to compare the values obtained as a function of altitude, i.e. temperature variations.

Materials and methods

Study areas

The three sites we studied (Figure 1) are the Puy de Sarcoui (trachytic lavas; volcano of pelean type; 1100 m altitude), the Montagne de la Plate (trachytic ash-fall deposits; 1500 m altitude) and the Puy de La Perdrix (trachytic lavas; 1780 m altitude). Stands were chosen according to the similarity criteria: (i) bedrock, (ii) slope (lower than 20°), (iii) exposure (south-west). Although the parent materials have different compactness – but not different chemistries – and greatly influence the initial pedogenesis velocity, resulting soils are quite similar and the results we obtained (see further) indicate that the comparison of sites on a climatic basis is acceptable. On the three sites, the soils are of andic type (volcanic soils of temperate climate at mountain level), but highly influenced by the podzolization process due to the acidity, the sandy texture of soil horizons and the high level of precipitation (Hetier 1971; Gueugnot et al. 1993).

The three sites are free of any sheep grazing pressure. The climate of the region is oceanic, the precipitation ranging from about 1000 mm year⁻¹ (Puy de Sarcoui) to 2000 mm year⁻¹ or more at highest altitudes, regularly spread throughout the year. The annual mean temperature is 6.4 °C, near the Puy de Sarcoui (data from the French Meteorological Institute), but cannot be accurately estimated at higher altitudes.

Methods

The sampling was carried out on large areas (>1 ha) on each site. This was done to avoid any data redundancy. However, the homogeneity of local conditions was carefully verified before sampling.

On each site, heather plants were randomly sampled in order to evaluate (i) the actual age distributions, (ii) the life expectancy, (iii) the layering probability as a function of the age. Altogether, 930 measures were done. A second phase evaluated some parameters of annual growth, biomass (standing crop) and nitrogen cycle. Firstly, we sampled the aboveground biomass of *Calluna* on five surfaces (0.25 m² each, leaves and supporting tissues) on each site. Then, on each site, we took 10 samples of soils (each in the first non-humic horizon, beneath the *Calluna* crowns: approximately 20 cm depth) in order to measure (i) the mean C/N ratio and (ii) the potential respiratory index giving an approximation of the soil ability to mineralize the organic matter. In the case of La Perdrix the patch structure of *Calluna* crown was recorded and mapped on one stand.

The *Calluna* age distribution and life expectancy were measured by counting under the microscope the annual growth rings of the biggest stem of alive and dead plants respectively. The same technique was applied to measure the layering probability, first, by estimating the mother-plant age and second, the layer stem age near its roots.

The biomass was weighed on dried harvested material (8 days, 60 °C, according to Clément's method, 1987) and the nitrogen parameters of current year stems and leaves were measured by the Kjeldhal method from 5 g from each of the same samples. All samples were collected by the end of the vegetation growth period.

The CO₂ productions (soil respiration) were measured during short-term incubations (28 days at 28 °C) of fresh soils. The soil moisture was adjusted to 85% of field capacity before incubation. The CO₂ accumulated in NaOH traps was measured after 7, 14, 21 and 28 days by titration (B. Godden, 1993, personal communication).

The C/N was measured by means of gas chromatography (C.H.O.N.S. Carlo-Erba).

Calluna extracts were obtained from leaves and stems (200 g). The material was ground and extracted twice in ethanol (2 l, 50% v/v) for 24 hours (4 °C) with constant shaking. After filtration, the extractive solution was evaporated under reduced pressure and then

desiccated. The remaining powder (yield 14.5%) was stocked in opaque receptacles and deep frozen before testing. Tests were carried out by means of aqueous and centrifuged solutions (6000 rpm for 10 min) in Petri dishes.

Seeds (*Agrostis tenuis*, *Phleum pratense*, *Achillea millefolium*, *Lotus corniculatus*, *Festuca rubra s.l.*, *Poa pratensis*, *Pinus sylvestris* and *Betula pendula*) were sterilized by 70% alcohol (2 min contact) and then moistened (24 h) in distilled and sterilized water. 1 ml of each concentration tested (see Results section) was introduced in the dishes, the moisture of seeds (25 seeds per dish) being maintained by means of a filter paper on the ground and the dishes stored in a saturated box. Illumination time was 16 hours/day at about 20 °C. Seedlings were daily recorded and removed.

Fungi (*Boletus granulatus*, *Boletus collinitus*, *Boletus luteus*, *Boletus edulis*, *Rhodopaxillus nudus*, *Laccaria laccata* var. *amethystina*, *Hebeloma crustiniforme*) were cultivated in sterilized conditions on Oddoux-Pachlewska medium. Inocula were stamped out by means of 8 mm diameter punches and put on the medium surface covered by a cellophane sheet, which avoids deep development of mycelium, and facilitates the fungus removal. The extracts were introduced in the medium (1 ml of different concentrations) during its cooling phase. Extracts for fungi were sterilized by filtration (Gellmann 0.45 μ). The resulting loss of this last operation was about 20% (w/w). Dishes were stored in dark conditions (20 °C) for 3 weeks. Fungi were then removed from the cellophane and immediately weighed.

Results

Demography of Calluna populations

A χ^2 test on demography results (Table 1) shows that the distributions of ages on Sarcoui and La Perdrix have some gaussian profiles. On the contrary, on La Plate site, the calculated χ^2 value is slightly more than the threshold value of the test and it is impossible to consider this distribution as gaussian. Previous works (Coquillard 1995) demonstrated that a sudden abandonment induces a very fast settlement of *Calluna* (16 to 20 years seem to be necessary to a complete covering) producing a typical bell curve of ages. Following this first phase, death and vegetative/sexual reproduction of the shrub modify the profile of ages which

Table 1. Demography of *Calluna* plants. Different letters in column m indicate statistical differences ($p < 0.05$). All measurements were done on different plants. n: sample size; m: average value; s: standard deviation; min: minimum value recorded; max: maximum value recorded; d.f.: degree of freedom. Parentheses show some absolute frequencies.

	Distribution of ages						
	n	m (year)	s	min. (year)	max. (year)	d.f.	χ^2 (calculated)
Sarcoui	130	16.43a	3.56	8 (1)	32 (1)	14	16.63
La Plate	183	17.77a	4.98	6 (1)	32 (2)	18	30.13
La Perdrix	115	12.19b	2.96	6 (1)	21 (1)	11	16.25

	Life expectancy						
	n	m (year)	s	min. (year)	max. (year)	d.f.	χ^2 (calculated)
Sarcoui	102	22.4a	3.72	15 (1)	34 (1)	14	11.99
La Plate	116	25.91a	3.32	17 (1)	34 (3)	13	9.75
La Perdrix	106	13.72b	2.54	8 (2)	24 (1)	10	6.09

Table 2. Mean age of *Calluna* layering on the three stands. Different letters in column m indicate statistical differences. n: sample size; m: average value; s: standard deviation; min: minimum value recorded; max: maximum value recorded. Parentheses show some absolute frequencies.

	n	m (year)	s	min. (year)	max. (year)
Sarcoui	35	9.37a	3.04	5 (2)	16 (1)
La Plate	27	10.78a	4.83	3 (1)	24 (1)
La Perdrix	27	6.59b	3.74	2 (4)	14 (1)

tends to become towards a uniform distribution in case – which is the more common – of a low reproduction rate. In such condition, the abandonment of grazing on La Plate seems to be older than on the two other sites.

The life expectancy differs significantly from the Sarcoui–La Plate sites to La Perdrix site. Briefly, this parameter seems to be stable from 1100–500 m alt. but presents an important decrease at higher altitudes. This is probably due to the alternance of falls and rises in temperature and multiple eliminations of the snow cover by wind, exposing the plants to the lowest temperatures during winter. In spite of these differences, the χ^2 test reveals that the death of plants obeys a normal law on the three sites (see the calculated χ^2 on Table 1).

Layering depends on several conditions: morphology (stems bending or not to the ground), physiology and gap proximity. Consequently, the average age of layering does not characterize the populations but rather the local conditions of growth. Inversely, the extremes (minimum and maximum ages) give important informations. *Calluna* seems able to layer in the early years of its life on our stands, from 2 to 5 years old (Table 2). Indeed, some experimental cultures demonstrate that this species is able to layer spontaneously at 6 months old (G. Mahy, personal communication). The oldest plants seem to be unable to layer on Sarcoui and La Plate sites. These observations must be linked to the crown structure on stands. On La Perdrix site, the short vegetation growth period (60 to 80 days/year) and the important snow cover make the heath ‘short legged’, prostrate, keeping the canopy low (20–30 cm high), so that the suitable conditions for layering are maintained throughout the plant life. Inversely, on the other stands the longer growth period and light competition induce height growth, sometimes up to 1 m tall. These observations are similar to those of MacDonald et al. (1995) who underlined that ‘the more prostrate stems which provide the potential for layering are likely to be suppressed when maximum canopy density is attained’. . . [our results indicate that layering is more frequent in stands of relatively young plants’.

Table 3. Biomasses and absolute annual productivity. Different letters in each column indicate statistical differences ($p < 0.05$). n: sample size. Values in columns 3 and 4 are weighed by the average covering (80% on Sarcoui and La Plate stands, 68% on La Perdrix stand).

	Biomass kg/m ² n = 5	Annual production of young stems, g.m ⁻² .yr ⁻¹ n = 10	Annual production of young stems, t.ha ⁻¹ .yr ⁻¹	Above ground biomass, t.ha ⁻¹
Sarcoui	1.85 ± 0.3a	473.1 ± 90.1a	3.78 ± 0.72	14.8 ± 2.4
La Plate	1.50 ± 0.26b	550.3 ± 104.4a	4.40 ± 0.83	12.0 ± 2.1
La Perdrix	1.05 ± 0.15c	390.9 ± 59.0b	3.13 ± 0.4	8.4 ± 1.0

Biomass measurements

Biomass dramatically decreases with altitude (Table 3). The total aboveground biomass was calculated taking into account the average heathland covering. The calculated biomasses are comparable to those obtained both by Doche (1983, 1986) on analogous stands in the Massif Central at 1000 m alt. (16.6 t ha⁻¹) and on one heathland in building phase in Scotland (Barclay-Estrup 1970).

The annual production of assimilating biomass does not significantly differ between Sarcoui and La Plate. On each of the sites the annual production of new stems represents an important amount of the total biomass (25–37%), and it is obvious that *Calluna* allocates more nutrients to supporting tissues at the lowest altitudes. The absolute annual productivity, ranging from 391–550 g m² year⁻¹, is higher than Aerts's measurements (290 g m⁻² year⁻¹) on harvested material from a dry heathland in the Netherlands, but is comparable to the results he obtained on a young stand (450 g m⁻² year⁻¹) (Aerts 1989, 1993).

Measurement of the main stems diameter (Figure 2) indicates a constant growth rate and proves that *Calluna* does not modify the proportions of nutrient allocation to its woody parts throughout its life, in contrast to woody species, such as Silver Birch, whose trunk diameter is limited by an asymptotic value (Prevosto et al. 1999a). Lastly, the decrease of the biomass of wood with altitude is consistent with the previous observations about the varying crown structures.

Elements of nitrogen cycle

The nitrogen concentration in the first year shoots (leaves + supporting tissues) does not vary in the same

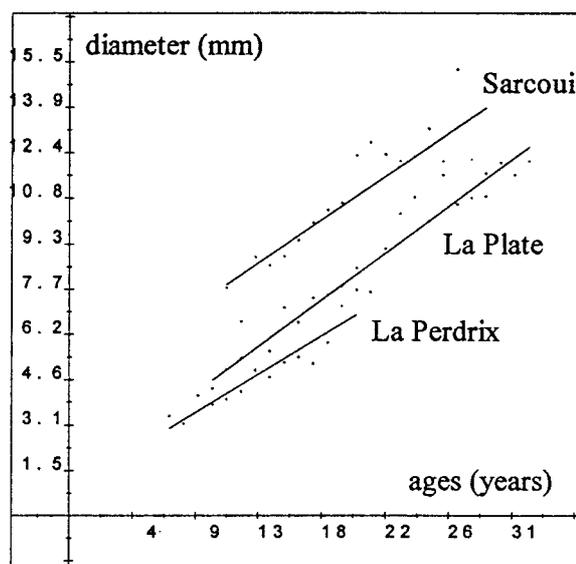


Figure 2. Diameter of the main stem of *Calluna* plants as a linear function of age on the three study sites. Sarcoui: $y = 0.33x + 4.22$; $n = 223$; $r = 0.87$; La Plate: $y = 0.36x + 0.99$; $n = 300$; $r = 0.97$; La Perdrix: $y = 0.29x + 0.89$; $n = 221$; $r = 0.94$.

Table 4. Absolute productivity of nitrogen. Different letters in each column indicate statistical differences ($p < 0.05$). n: sample size. Annual nitrogen absorption are weighed by the mean covering (80% on Sarcoui and La Plate stands, 68% on La Perdrix stand).

	Total Nitrogen ‰ n = 5	Total nitrogen g.m ⁻²	Annual nitrogen absorption kg.ha ⁻¹
Sarcoui	14.12 ± 1.25a	6.67 ± 0.11a	53.36 ± 0.88
LaPlate	12.31 ± 0.71a	6.77 ± 0.07a	54.16 ± 0.56
La Perdrix	13.28 ± 0.97a	5.19 ± 0.06b	35.42 ± 0.04

Table 5. C/N ratio. Different letters in each column indicate statistical differences ($p < 0.05$). n: sample size.

	%C	%N	C/N ($n = 10$)
Sarcoui	8.24a	0.48a	$17.00 \pm 1, 07a$
La Platte	13.83b	0.90b	$15.35 \pm 1, 15b$
La Perdrix	15.20c	1.10c	$13.78 \pm 0, 37c$

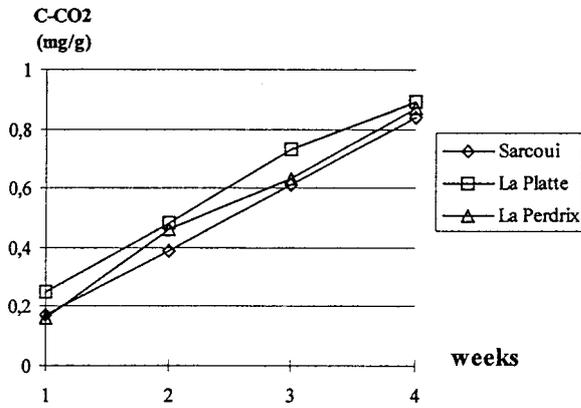


Figure 3. Cumulative C-CO₂ (mg g⁻¹ of soil) production recorded on four weeks.

way as biomass, being equivalent on the three sites (Table 4). The nitrogen concentrations are similar to the results obtained by Aerts (about 14‰); one may consider that these values constitute a characteristic of *Calluna*. The study of Aerts demonstrated that nitrogen concentrations of shoots do not vary significantly during the growing season but lightly increase in winter (from 14‰ to 20‰) and the experiments he carried out indicated that *Calluna* does not change nitrogen concentrations in current year leaves as a function of nutrient availability even in the case of high nutrient fertilization (4NPK), the leaf N concentrations being stable.

Considering the nutrient resources, the stock of organic matter in soils increases significantly with altitude as commonly observed (Table 5). Surprisingly, the C/N ratio decreases, this indicating better conditions for mineralization at highest altitudes. Figure 3 shows that the microbial populations have comparable potentialities so that the better mineralization observed may be related to climatic conditions, particularly water availability which could compensate the shortest period of suitable growth conditions.

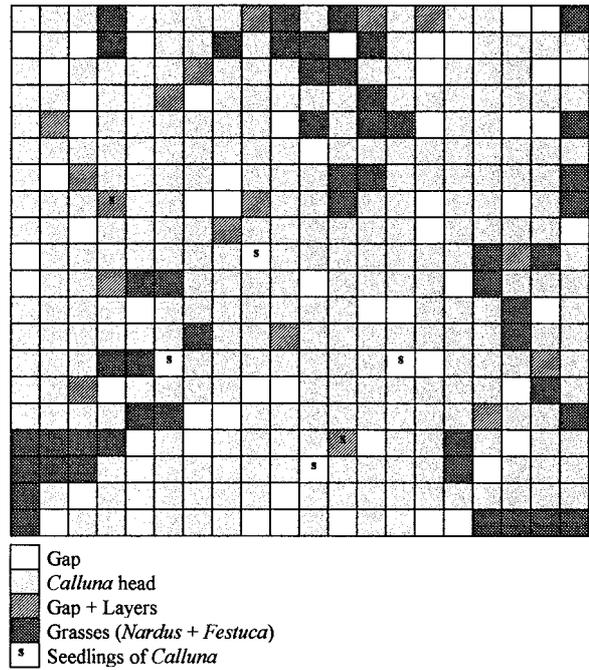


Figure 4. Patch structure of La Perdrix stand (100 m²).

Table 6. Percentages of gaps and percentages of recently colonized gaps.

	Gaps	Gaps with seedlings	Layers and gaps with layers	Gaps with other species
Sarcoui	–	–	?	–
La Platte	10%	–	3.8% (24%)	4%
La Perdrix	19%	1.5 %	4% (23%)	12.5%

Patch structure

It has been demonstrated that the patch structure strongly depends on the phase of *Calluna* populations (Barclay-Estrup & Gimingham 1969; Barclay-Estrup 1970; MacDonald et al. 1995). In our case the Sarcoui site presents a *Calluna* population in a mature phase, i.e. free of gaps. Inversely, La Platte and La Perdrix sites are in a steady state which exhibits some gaps. La Perdrix site seems to be the most advanced, and numerous gaps are visible (Figure 4).

In addition, gaps can be colonized (Table 6) either by *Calluna* seedlings or by grasses (*Nardus stricta* and *Festuca rubra* s.l.) on La Perdrix. We never observed this phenomenon on other sites, excepted on a stand we previously studied on which erosion was very active (Coquillard & Fain 1995).

Inhibition of colonization by action on germination and mycorrhizae

The presence of *Calluna* seedlings and the increase of substitution by grasses at highest altitudes might be related to the variable inhibitory action of an allelopathic factor produced by *Calluna* litter and reported by numerous authors (Ballester et al. 1975; Salas & Vieitez 1975; Marcelis 1981; De Hullu & Gimingham 1984; Heil 1984 in Bruggink 1993). This factor is known to inhibit *Calluna* seed germination as well as that of several grasses and woody species. Several experiments were engaged by these authors to identify and quantify the inhibiting action of different parts of the heather. However, despite the presence of several identified products (acids: *p*-coumaric acid, vanillic acid; coumarins: aesculetol; phenols: hydroquinone; flavonoids: quercetin), none of them can clearly be made responsible for the very weak percentages of emergence commonly observed in heathlands. In fact, many authors do not agree with the inhibition theory (Marcelis 1981; Bruggink 1993) but emphasize the importance of some microecological factors such as pH (Helsper & Klerkken 1984), dryness, red/red-far light ratio under *Calluna* canopy and substrate compactness (Werger et al. 1985). The results we obtained (Figure 5) on germination corroborate those of Ballester et al. (1975) and Marcelis (1981) showing that in most cases the concentration of *Calluna* extracts needed to obtain a significant inhibition is almost 50 mg ml⁻¹. A simple calculus from the extraction yield (11.6%) demonstrates that such a concentration is quite unlikely in the field. Assuming a 10 cm litter thickness in a heathland in a steady state and a complete availability of the inhibiting factor it contains, the resulting concentration would be one hundred times less than that required.

Bruggink (1993) observed the non survival of established *Calluna* seedlings in heathland despite the numerous emerged seedlings (1480 m⁻²) he recorded one year before. Indeed, we noticed that quite low concentrations of the active extract are capable of inhibiting the hypocotyle elongation of *Solanum lycopersicum* we chose as biological indicator (Table 7).

Robinson (1972) obtained inhibitions of mycorrhizal fungi growth using some *Calluna* roots leachings. We obtained similar results in several cases with our extracts (Table 8). Some fungi seem to be very sensitive to extract compounds (*Boletus collinitus*, *B. granulatus*, *B. luteus*, *B. edulis*, *Rhodopaxillus nudus*) but *Laccaria laccata* and *Hebeloma crustilin-*

iforme were not. It is very important to emphasize that these sensitive fungi are known to be mycorrhizal with *Pinus sylvestris*. On the contrary, *L. laccata* and *H. crustiliniforme* are mycorrhizal fungi of birch seedlings (Perala & Alm 1990). It has been demonstrated that mycorrhizal birch seedlings survive and grow better than non-mycorrhizal ones (Dighton 1983; Frankland & Harrison 1985, in Perala & Alm 1990).

Discussion, elements for *Calluna* modelling

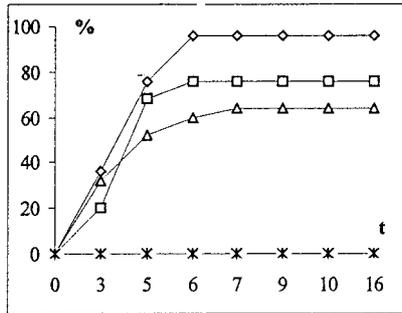
In this section, we will review some parameters and model assumptions we draw from the Results section. The modelling technique we choose (Discrete Event Simulation) in order to take into account the spatial effects implies that the model initialization and sub-models would respect several constraints:

1. To initialize the data structure (an array analogous to a grid of a cellular automata) with the real patch structure recorded.
2. To initialize the age of *Calluna* plants with a distribution equivalent to that fitted.
3. To take into account the recruitment and death processes, that is to say to estimate for each individual, from year to year, the surviving probability.
4. To take into account the local neighboring in the computation of layering and germination success probabilities on a given gap.

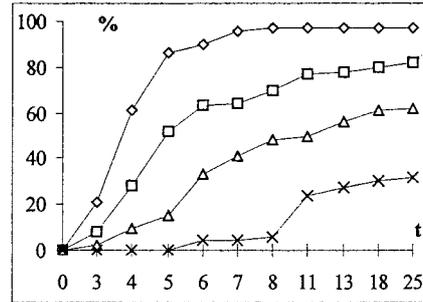
Temperature rising

One of the main problems of modelling vegetation change driven by climatic variations consists of estimating the rising temperature as a function of time. Most authors generally adopt a linear relation. Beuker et al. (1996) retained 0.04 °C as the slope of the linear function of temperature over 100 years; Monsrud et al. (1996) retained 0.26 °C per decade. In our case according to most of the general circulation model results, we adopted a linear rising of 2 °C from now to the year 2020. Consequently, the parameters modifications we retained will obey this linear relation.

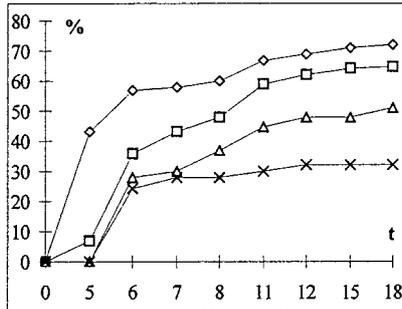
Lastly, given that the altitude variations correspond to a linear variation of the mean annual temperature (0.5 °C/100 m), the results obtained at the lowest altitude can be transposed as model inputs for the higher stands we intend to simulate.



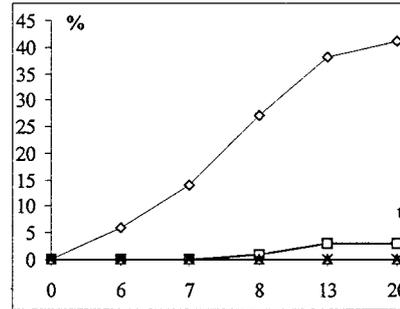
Agrostis tenuis



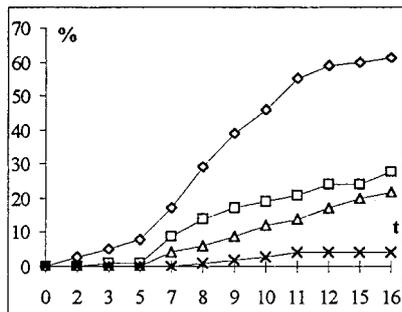
Phleum pratense



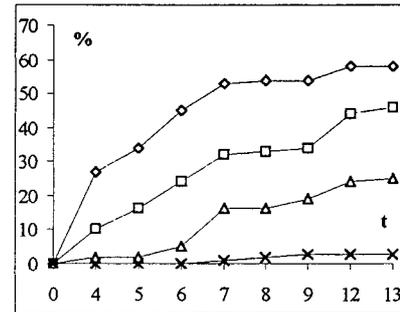
Festuca rubra s.l.



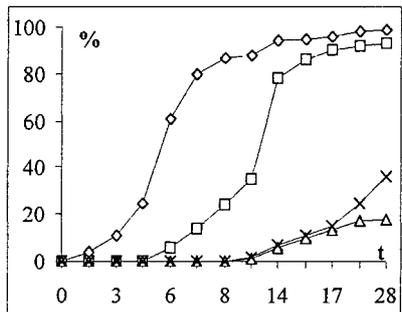
Poa pratensis



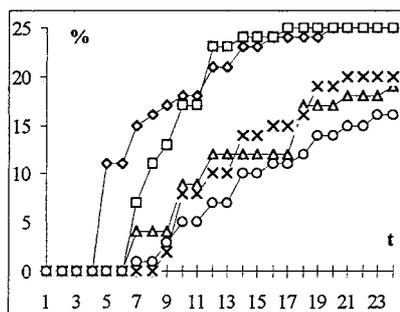
Achillea millefolium



Lotus corniculatus



Pinus sylvestris



Betula pendula

Figure 5. Kinetics of germination (in percentage) of several species under different concentrations of *Calluna* extracts: \diamond : control; \square : 10; Δ : 25; \times : 50; \circ : 100 ($\text{mg}\cdot\text{ml}^{-1}$ of extract). t: time in days. For each species and concentration $n = 100$.

Table 7. Inhibition to hypocotyle elongation (*Solanum lycopersicum*) under various concentrations of *Calluna* extracts. Letters indicate statistical differences ($p < 0.05$; $n = 15$).

mg/ml	Control	0.1	0.25	0.5	0.75	1	2.5	5	7.5	10	25
Elongation (mm)	17.45	19.97	18.04	14.52	12.68	9.8	8.06	5.89	5.74	5.42	4.36
	$\pm 1.97a$	$\pm 2.3b$	$\pm 2.1b$	$\pm 4.0c$	$\pm 2.16c$	$\pm 2.03d$	$\pm 1.55e$	$\pm 1.14f$	$\pm 0.96f$	$\pm 1.57f$	$\pm 0.68g$
% inhib.	–	–	–	27	27	44	54	66	67	69	75

Table 8. Fungi growth inhibition (%) under different concentrations of *Calluna* extracts (for each concentration, $n = 4$).

	mg/ml	0.08	0.2	0.4	0.8	1.2	2.0	4.0	8.0
<i>Boletus granulatus</i>		13	21	21	44	59	–	89	92
<i>Boletus collinitus</i>		0	0	0	59	59	59	59	54
<i>Boletus luteus</i>		4	7	20	50	60	–	–	–
<i>Boletus edulis</i>		8	0	36	54	–	–	–	–
<i>Rhodopaxillus nudus</i>		18	25	25	43	–	–	–	–
<i>Laccaria laccata</i>		0	0	0	0	0	14	–	–
<i>Hebeloma crustuliniforme</i>		0	0						Stimulation of growth

Life expectancy

As mentioned above, a normal law seems to be an acceptable assumption for modelling *Calluna* death probabilities. Previous investigations resulted in the same conclusion (Coquillard & Hill 1997). According to the previous remarks we obtain the linear relation:

$$LE = 13.72 + 5.25 * t, t \in [0, \dots, 2]$$

where LE = mean life expectancy (years) and t = temperature ($^{\circ}C$).

Adventitious rooting probabilities

The layering probabilities are linked to two main parameters: (i) the heathland structure (MacDonald et al. 1995), the structure influencing the layering probabilities as a function of age, and (ii) the gap surrounding. Thus, we propose that the layering probabilities be modelled in an acceptable manner by means of a normal law, these probabilities being in a linear relation with the biomasses:

$$ML = 10.75 + 16 * 10^{-2} * b \quad b \in [0, \dots, 679]$$

where ML = mean age of plants for layering (year) and b the increase of biomass (g).

The maximum probability of layering is attained when every neighbouring plant to a gap has the optimum age to do so. The probability of a layering event (P_l) can be computed by:

$$P_l = \sum_n P_i \quad i \in [1, \dots, n] \quad \text{and} \quad 0 \leq P_l \leq 1.$$

where n is the number of neighbours.

Table 6 indicates that 23% of gaps present some layers. The average percentage of cells occupied by living plants and surrounding the gaps equals 70% (La Perdrix stand). So we can establish the layering probabilities of a gap as a linear relation with the number n of living neighbours:

$$P_n = n * 6 * 10^{-2}$$

where P_n = probability of layering event.

This last relation leads to estimate the maximum probability (P_6) to 0.36 – using an hexagonal compact structure as meshwork in the model (see Coquillard 1995). This is an approximation and we suspect that this value is underestimated. More investigations could be engaged to get some accurate values of layering probabilities but would require obtaining statistical values for every possible combination of ages and number of neighbouring plants. We fear that numerous samplings would cause great damage to the sites so that it would not be recommended in the protected area of the Volcanoes Park of Auvergne. Finally, the layering probability on a gap (P_g) can be written as:

$$P_g = P_l * P_n$$

Inhibition of seedlings survival

We noticed that a small number of established seedlings of *Calluna* was present on some gaps at La Perdrix site. However, our experiments showed the complete inhibition of hypocotyle elongation of *Solanum lycopersicum* and other species by litter compounds, even if germination was not completely inhibited by weak concentrations. Thus, we propose the hypothesis that seed germination is probably due to the high level of precipitation at subalpine level progressively eliminating most of the litter (gentle erosion) and leaching its remaining part. Indeed, our experiments demonstrated that a one hundred percent of inhibition of germination (*Lotus corniculatus*) was completely reversible by simple water washing. This leads to suppose that some soluble compounds such as catechic tannins or quercetin (one HPLC experiment revealed that quercetin was probably one of the most represented compound) could be good candidates for such a role. Assuming that no important decrease of precipitation could occur at subalpine level, it is supposed that no significant variations of *Calluna* seeds germination probabilities would take place in the next decades. Consequently, we fixed this probability to its present value, i.e. about 2%. Naturally, the layering and the sexual reproduction are processes in competition in the model. Concerning the other species, the same assumptions are applied to grasses, and the inhibitory factor action on Silver Birch and Scots Pine will be indirectly integrated in the recruitment model by means of the number of established seedlings per year and per tree recorded on stands.

Biomass increase

Introducing a true model of individual growth of *Calluna vulgaris* would imply a dramatic increase of time computing and model complexity. Indeed, a realistic model of *Calluna* growth would imply taking into account not solely the time but the effect of competition for space between neighbouring plants. In this case, the implementation of such a process would result in calculating the growth of about 20 400 individuals (and checking the attributes of the neighbours of each of them), at each time step of the simulation, for a simulated stand of 100 × 100 m. In addition, from a technical point of view, this process would introduce some severe programming constraints, particularly in solving the problem of parallelism between neighbouring plants growing at the same moment. This would result in prohibiting run time simulation

Table 9. Actual and predicted equilibrium biomasses on the two highest stands. T = mean residence time of nitrogen.

	N availability	T	Actual biomass	Predicted biomass
La Plate	6.77 (unchanged)	2.72	1500	1520
La Perdrix	5.19 → 6.77	2.48	1050	1729

and consequently disallow any experiments involving a sufficient number of replicates to compute reasonable confidence intervals of results. Thus, we chose an aggregated model which allows estimating the global biomass of *Calluna* from the demography results and colonized surfaces on the stand. Doing this, we introduce an additional assumption: the heathland is supposed to be in a steady state. It is the case on the sites we studied and we intend to simulate. Biomass modifications induced by a rise of temperature can be inferred from Aerts's relation (Aerts 1993) which predicts the equilibrium biomass of *Calluna* (i.e. the average biomass in a steady state heathland) as a function of the nutrient availability:

$$B = \frac{NTE}{C}$$

where B = equilibrium biomass (g m^{-2}), N = nutrient availability ($\text{g m}^{-2} \text{ year}^{-1}$), E = nutrient uptake efficiency (dimensionless), T = mean residence time of nitrogen (year), C = plant nitrogen concentration (g g^{-1}). Calculated results (Table 9) were obtained using *ad minima* hypothesis:

1. In case of the steady state of the heathland, the litter production is quite similar to the absolute annual productivity of stems and leaves, i.e. annual nutrient uptake equals annual nutrient loss (Aerts 1993; Wallen 1980).
2. The nitrogen availability increases in the same way as temperature and the future nutrient availability will be at least equal to the annual uptake we recorded at 400 m alt. lower.
3. The mean residence time of nitrogen is calculated as the ratio between the average amount of nitrogen in the plants and the annual uptake. In this case, we used the nitrogen content of young stems and leaves as annual uptake, neglecting the annual amount of nitrogen used to ensure the annual growth of stems without leaves and consequently slightly under-estimating the equilibrium biomass.

Establishing the linear biomass rising at La Perdrix as a function of temperature we obtain:

$$B = 1050 + 339.5 * t, \quad t \in [0, \dots, 2]$$

where B = equilibrium biomass (g m^{-2}) and t in $^{\circ}\text{C}$.

Conclusion

Numerous improvements could be brought into modelling assumptions – in the linear models presented here and the aggregated simulation model too – sampling and analysis of data as well. However, previous simulations by means of DES of heathland functioning gave encouraging and satisfactory results: some partial validations of the simulation results (confrontation validation, empirical validation, repetitivity validation (Hill et al. 1996; Coquillard & Hill 1997)) were successfully engaged.

Surprisingly a simple review of the results reported above allows to suppose that the settlement of Silver Birch and Scots Pine would not be favoured by a warming climate. On the contrary, the induced increase of biomass and change of *Calluna* forms (from prostrate form to hemispherical form (MacDonald et al. 1995)) would slow down the settlement of this species and possibly prohibit any change of vegetation for a long time. On the other hand, the pastoral value index of presently sheep grazed heathlands would drastically decrease and endanger the pastoral practices which are one of the main (maybe the unique) tools for upland management.

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