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Simulation of the cyclical process of heathlands: induction of mosaic structures, evolution to irreversible states

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Abstract

A simulation (random process with a discrete control of time) of cyclical regeneration of the monospecific heathlands established on the volcanic Chaîne des Puys (Massif Central, France) after the general and sudden surrender of grazing in the middle of this century, is proposed. On the high sloping zones on the south and south-west, spontaneous regressive dynamics of the heathlands appears, causing intense erosion. In other cases, some mosaic structures (*Calluna vulgaris-Brachypodium pinnatum*) cover the volcanoes. This highly simplified model takes into account the following processes: (i) the senescence process and vegetative reproduction of *Calluna*, (ii) the reproduction and intraspecific competition of *Pinus sylvestris*, (iii) erosion. The main results demonstrate that such a system exhibits an oscillatory behaviour. This phenomenon is strongly dependent on the initial parameters of the *Calluna* populations and may or may not reach an interior equilibrium: a stationary phase. An activity state function, taking into account the average transformation rapidity and modifications with constant surfaces, allows following the whole activity of the system. The origin of the mosaics could lie in this behaviour and could be more clearly topologic than strictly ecological. The oscillatory behaviour induces a multiple-steps settlement by pines. The suspension of grazing in several times would favour the heath colonization by multimodal age-population of *Calluna* and then lessen the oscillations as well as erosion and regularizes pine colonization. The optimal density of the initial pool of pines seems to be equivalent to 1 tree per 700 m².

Keywords: Erosion; Heathlands

1. Introduction

The ecosystems studied are situated in the Chaîne des Puys (a high esthetic/biologic value and well-known landscape), in the Massif Central (France). The chain is constituted by a set of about 60 volcanoes, north-south lined up at about 1100 m altitude, 35 km long and 3 or 4 wide. The latest eruption probably traces back to 6000 years B.P., maybe less.

After the general and sudden suspension of sheep grazing in the middle of the century, some important monospecific heathlands were established on the south and south-west exposed sides of the volcanoes. Those slopes actually show an

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important erosion. Some earlier works (Coquillard and Gueugnot, 1991; Coquillard, 1993) demonstrated that this phenomenon of heathland degradation is strongly dependent on multiple synergetic factors such as: the traditional cultivation of the volcanoes, grazing with no restitution of dungs by night-folding in flat and arable zones causes a significant impoverishment of the soils nutriments (Loiseau et al., 1990); the great instability of the fluffy andosoils and substrate (scorias and ash-fall deposits); the degree of the slope (about 25°) and its thermophilic exposure; the action of an allelopathic factor of Calluna vulgaris that inhibits mycorrhization and seedling growth (Robinson, 1972; Salas and Vietez, 1975; Coquillard, 1993); the remoteness of trees often preventing the slopes from any phanerophytic settlement.

The 30-35 year old heaths, which developed after the grazing in these conditions ceased, show some increasing bare spots – as the senescence process of the *Calluna* heads goes by (Barclay-Estrup and Gimingham, 1969; Doche, 1986) – falling in large and bald areas, ending in a complete erosion of the volcano versant.

Lastly, some large surfaces of mosaic vegetation, constituted of *Calluna vulgaris* and *Brachypodium pinnatum* areas, cover the gently sloping zones (lower than 25°) remote from *Pinus sylvestris* influence.

The two types of vegetation, degraded heathlands and mosaics, have already been studied from ecological and syntaxonomic points of view (Lemée and Carbiener, 1956; Michalet et al., 1988; Coquillard et al., 1988a,b; Coquillard and Gueugnot, 1991; Coquillard, 1993).

2. Biological model and algorithm

2.1. Markovian assumptions

Several studies about the cyclical evolution of heathlands, particularly the post-fire regeneration, have already been proposed (Legg, 1980; Hobbs, 1983; Hobbs and Legg, 1983; Lippe et al., 1985), using the Markovian approach. But as Lippe et al. observed: "The results of these anal-

yses where mixed, the model appearing to be useful in some, but often being subject to several problems, including non-homogeneity of the transition probability matrix and spatial influences. Two significant practical difficulties are the definition of the states, and the measurement of real (rather than inferred) transition probabilities". One of the most important difficulties is that of estimating the transition probabilities, because the rate of vegetation change is not fast enough to be measured in a reasonable amount of time: 20 years at least being necessary to constitute the data set. Finally, the transition probabilities would be influenced by the spatial effects, particularly the seed-parent plant distance, abundance and patch structure of the species.

2.2. Biological model

These considerations and the purpose of modelling at the same time the Calluna vegetative reproduction and the possible pine influence led us to leave the Markov assumption, i.e. changes at a certain point are independent of the changes at neighbouring points, and to attempt to simulate the cyclical process of heath regeneration with the Monte Carlo method (a computer random process with a discrete control of time, widely used in several industrial domains such as the simulation of producing systems) as Luan et al. (1992) did. The biological model (Fig. 1), highly simplified, takes into account a set of parameters presented hereafter. These parameters have been sampled on different stands or drawn-up from the bibliography (Coquillard, 1993; Coquillard and Fain, 1995).

The main parameters are:

- The age-distribution of the initial population of *Calluna*. The profile is of Gaussian type, with the following parameters, measured on an heathland in mature phase: M (mean) = 14.6 ± 1 and σ (standard deviation) = 3.6 years. The values M = 16 and $\sigma = 4$ have been retained in the simulations. The case of a bimodal profile has also been studied, this corresponding to a surrender of grazing in two steps.

- The vegetative reproduction of *Calluna* by means of layering (Mohamed and Gimingham,

1970; Gimingham, 1978; Doche, 1986): 10 to 20% observed in cases of eroded heathlands in the Chaîne des Puys.

- The intensity of erosion. We estimate, by measurement on stands, 9 years would be necessary to obtain a complete erosion of soil of 45 cm thick. We assumed that the velocity of erosion is a constant. This is an approximation.

- The colonization process by *Pinus sylvestris*, including the seed distribution, germination, growth process and the effect of soil immobilization by roots.



Fig. 1. The figure presents the ecosystem model as a finite state machine, where the circles represent the intervening states and the rectangles represent the final states. Arrows indicate the possible transitions, the numbers the durations of the transitions. The state V corresponds to the initial state, i.e. the alive state of the initial Calluna populations; S is the senescent state of Calluna heads, generally called gaps; C the coalescent gaps, which are the scene of erosion; M the lavered Calluna heads; g the germination of Pinus and the young trees of less than 5 years old; P1 the juvenile trees of less than 20 years old; P2 the pine of 20 years old; Pr the grown-up trees, that is, the seed distributors; D the eroded gaps; and a the elements of the rings surrounding the pines and simulating the influence of roots. We notice that every intervening state is able to be affected by the pine roots (a state), this allowing the simulation of the immobilization of the soils and the competition between the trees.

The pine settlement is brought into operation by calculation of the germination probability. The algorithm of the germination occurrences is the following:

WHILE (ratio germination/tree ≤ 0	.6) DO
FOR every grown-up tree (randomly chosen in a list) DO
FOR every plot (S	S or C state, randomly chosen in a list) DO
Calculati	on of the distance tree-plot: d
IF (3 < $d \le 20$) THEN	
	Calculation of the germination
	probability: <i>p</i>
	Generation of a random number:
	$h \ (0 \le h \le 1)$
	IF $(h \le p)$ THEN germination = true
	ELSE germination = false
	ENDIF
ENDIF	
ENDFOR	
ENDFOR	
ENDWHILE	

The germination probability p is calculated by means of the Gaussian distribution (Fig. 2) with the parameters: mean = 0.0 m, standard deviation = 9.9 m, the distance d and the total number of seedlings observed per pine (average number of germinations observed) = 34. No germination can be detected within a 3-m radius around a pine (all parameters drawn-up from Guittet and Laberche, 1972,1974). The average survival rate of the seedlings, i.e. the juvenile trees still alive after 4 years, is equal to 0.6/grown-up pine/year (sampled from *Calluna* stands in degenerate phase).

The simulation of soil immobilization by roots is realized by rings, surrounding the pines, which are age-dependent. This also allows, at the same time, the simulation of competition between the trees. The diameter of the rings increases by 3 times: the pines younger than 5 years have no ring, the pines older than 5 and younger than 20 a ring of 2.1 meters diameter, the grown-up trees a 3.5-m one. The juvenile-grown-up transition is set up at 20 years.



Fig. 2. Seed distribution profile of *Pinus sylvestris* (σ = standard deviation). 95% of the seed are distributed within a radius of 19.8 m.

2.3. Computer data structure and implementation details

The software, written in C + + and Oriented Object Pascal, is organized as a set of modules and include files:

- graphic libraries for the landscape display or drawing mathematical results.
- interface modules.
- computing kernel called MODCAL.

The computer data structure used to store the state of the global stand is an array $(100 \times 50 \text{ of reals})$ where the hexagonal structure we chose as meshwork (each plot (0.7 m of average diameter measured) is surrounded by six others) is saved (Fig. 3). The central area allows us to follow the evolution of the pine settlement from variable initial distances of the seed distributors.

Each simulation is carried out over 200 years and repeated 16 times according to the central



Fig. 3. A. The RAM representation of the stand is an array (100×50) . The central area allows us to follow the pine settlement from variable initial distances. B. The hexagonal-compact structure: the plot (I,J) is surrounded by 6 neighbours.

limit theorem results in order to obtain the best approximation of the means computed with a great number of simulations ($N \ge 30$). This is usually called the "replication technique" by the computer simulation community and allows the calculation of confidence intervals.

The simulating kernel, a sequential one, is directed by events. Consequently, the annual cycle goes off in four steps:

- i. Senescence events.
- ii. Layering events.
- iii. Pine reproduction: implementation of germinations, bring the rings and statements of trees up to date.
- iv. Bring the D states up to date, computation of statistic parameters.

3. Results

3.1. Topologic origin of the mosaics

First we studied the system in the case of no erosion and no action of *Pinus sylvestris*. The results (Fig. 4a and 4b) have been obtained by increasing the *Calluna* layering rate from 10 to 90%. In case of a layering rate lower than 40% the system reaches an interior equilibrium, a stationary phase, showing a damping-down phenomenon. In case of a rate higher than 40%, the system exhibits a rhythmic behaviour, the damping-down effect having disappeared.

This oscillatory behaviour and the bifurcation constitute a characteristic of a complex non-linear system, already described by numerous authors on the subject of the ecosystem dynamics



Fig. 4. Layered surfaces (4a) and bare-soil surfaces (4b) as functions of time. The different curves correspond to the *Calluna* layering rates varying from 10 to 90%. Initialization parameters: one population (M = 16, $\sigma = 4$), no erosion.

(Pacala and Silander, 1985; Pakes and Maller, 1990; Rinaldi and Muratori, 1992,1993). In other respects, one of the most important consequences

results in the alternation of about 5 years stationary phase (the peaks and troughs of the curves), where the system exhibits no activity or nearly no activity, and 15 years excitation phase (the slopes). This alternation is described more detailed hereafter (see section 3).

This rhythmic behaviour has some important repercussions on the vegetation structure of the heathland, and we propound the hypothesis that the origin of the mosaics we observed lies in that behaviour.

Indeed, if we observe the profile of the ages along a line across the area (Fig. 5a), we note that some large and lasting gaps appear, corresponding to the *Calluna* death periods. The colonization of the gaps by an herbaceous species, *Brachypodium pinnatum*, holds up the cicatrization of the heathland and induces the coexistence of the two structures. This phenomenon, rhythmic behaviour and mosaic structure, is already apparent in the works by Legg (1980) using the Markovian approach of the heathland as a mosaic vegetation.

In other respects, as we could have supposed, there is a tendency for the phenomenon to disappear as the layering rate increases (Fig. 5b). Consequently, the origin of the mosaic vegetation would be more clearly a topologic one, because of its dependence on age-distribution, than strictly an ecological one.

3.2. Action of erosion and pine colonization

The introduction of the erosion parameter, which corresponds to a significant slope and a thermophilic exposure, induces an irreversible state of the system. We immediately remark (Fig.



Fig. 5. Age profile along a line across the stand between the abscises 10 and 40 between 50 and 64 years by steps of 2. The arrows point to the gaps. a: layering rate = 10%. b: layering rate = 60%.

6) the progression of the eroded surfaces by multiple steps, according to the rhythmic behaviour. The stationary phases are synchronic with the peaks of the layering curve and the troughs of the coalescences one.

By an other way, the presence of two initial *Calluna*-populations, at 10 years intervals, greatly smooths the oscillations, and the system reaches its equilibrium in a regular way (Fig. 7). Inversely, the initialization of the model with only one population which standard deviation $\sigma = 2$ emphasizes the oscillations.

Moreover the settlement of the pines obeys this scheme. In the two cases (10 or 60%, Fig. 8a and 8b) the optimal number of initial trees seems to be 3, that is to say a density equivalent to 1 pine per 700 m².

Fig. 9 shows that the increase in the initial

density of pines does not induce any better colonization whatever the layering rate may be.

The pine settlement has some important repercussions over the erosion rate, falling down from 93% to 43% (Fig. 10). The slowness of the colonization (Fig. 11) of such an ecosystem as we simulated corroborates both the different results from the french Massif Central by Doche (1986), who observed 18 germinations/ha/year in such an ecosystem, and from Scotland by de Hullu and Gimingham (1984), who found a decrease from 60% in any *Calluna* phases to 6% in the degenerate one.

3.3. State activity of the system

From a fundamental point of view as well as from a management one it would be interesting



Fig. 5 (continued).



Fig. 6. Evolution of eroded (D), layered (M) and bare-soil (S + C) as functions of time (one initial population M = 16 years and $\sigma = 4$ years, erosion intensity = 9 years).



Fig. 7. Layered surfaces as a function of time. Erosion rapidity: 9 years. Three cases are considered: 1. One initial *Calluna*-population $(M = 16; \sigma = 4)$. 2. One initial *Calluna*-population $(M = 16; \sigma = 2)$. 3. Two initial *Calluna*-populations $(M = 16; \sigma = 4)$ at 10-year interval.



Fig. 8. Number of grown-up trees (N) as a function of time in case of 10% (a) and 60% (b) of layering rate (one *Calluna*-population, M = 16, $\sigma = 4$). The numbers indicate the size of the initial pool of pines.



Fig. 9. Number of grown-up trees (N) on the whole stand as a function of the initial pool of pines: N = f(i), in different cases of layering rate (from 10 to 90%). Simulations over 200 years, one initial *Calluna* population (M = 16, $\sigma = 4$), no erosion.



Fig. 10. Eroded surfaces on the central area as a function of time (one *Calluna*-population, M = 16, $\sigma = 4$, 10% of layering rate). 1: one initial pine at 18 m distance. 2: one initial pine at 3.5 m distance. 3: one initial pine centred. 4: same conditions as 3 but two initial *Calluna* populations at 10-year interval.

to quantify the system activity accounting for the stationary and activity phases. To this end, we will first consider the transformation rapidity of each present state:

At one given time:

$$\sum_{i=1,n} V_i = 0$$

where V_i = slope of the *i* curve of the *i* state, *n* = number of states and

$$\sum_{i=1,n} \left(V_i \right)^2 \ge 0.$$

The average transformation rapidity at the "t" instant (t year) is:

$$V_t = \sqrt{\Sigma(V_{ti})^2} / n$$

 $V_t = 0$ in case of equilibrium.

Secondly, when the system reaches the equilibrium, the slopes (V_i) are nil but some modifications, with constant surfaces, persist. Let us take

into account these modifications by the expression:

$$M_t = \left(\sum_{j=1,N} P_{tj}\right)/n,$$

where $P_t = \text{plot}$ having been modified at the t instant. N = total number of plots on the area.

 M_t is nil (or nearly) during the stationary phase, and became quite constant at the equilibrium.

The activity state function can be written:

$$E_t = V_t + M_t$$

and

$$E_t = \frac{\sqrt{\sum_{n} \left(V_{ti}\right)^2} + \sum_{N} P_{tj}}{n}.$$

The system does not reach any equilibrium and exhibits a cyclic behaviour in the case of 60% of *Calluna* layering rate and no erosion (Fig. 12a). The peaks correspond to the maximum ac-



Fig. 11. Number of grown-up trees (N) on the central area as a function of time (one *Calluna*-population, M = 16, $\sigma = 4$, 10% of layering rate, erosion rapidity = 9 years). 1: one initial pine at 18 m distance. 2: one initial pine at 3.5 m distance. 3: one initial pine centred.







Fig. 12 (continued).

tivity and the troughs to the stationary phases. Inversely, in case of a 10% rate (Fig. 12b), the activity progressively declines to become more or less a constant and the average transformation rapidity (V_t) tends to 0.

In case of erosion and pine development the two functions (E_t and V_t) tend to 0 (Fig. 12c) because of the irreversibility of the process (we did not simulate the turnover process of pines and herbaceous layer).

4. Conclusion

We can assume that the surrender of grazing by multiple steps would greatly smooth the oscillations of the *Calluna* ecosystems, favour the pine settlement and prevent too much erosion. That, and the implantation of pines with a density of one pine per 700 m² would be a good technique to prevent any important damage on every zone

Fig. 12. Activity state function (description in text).

^{1:} $E_t = (\sqrt{\sum_n (V_{ti})^2} + \sum P_{tj})/n$

^{2:} $V_t = \sqrt{\sum_n (V_{ti})^2 / n}$.

a. The system exhibits cyclical behaviour; one initial *Calluna* population (M = 16, $\sigma = 4$), layering rate = 60%, no erosion. b. The system reaches an equilibrium; one initial *Calluna* population (M = 16, $\sigma = 4$), layering rate = 60%, no erosion. c. The system reaches an irreversible state; one initial *Calluna* population (M = 16, $\sigma = 4$), layering rate = 10%, erosion rapidity = 9 years, one initial pine.

analogous to the Chaîne des Puys stands in the Massif Central.

Some numerous improvements could be brought into the algorithm such as the introduction of *Calluna* death probability (increasing from 0 for the one year old heads to 1 for the 30 aged heads), the layering potentialities as a function of time, variations of the erosion intensity, implementation of a true *Pinus sylvestris* forest growth model, etc. In these domains the lack of biological data still remains, when technical problems seem able to be more or less easily solved.

This method presents some numerous advantages, the most important of which is to take into account the spatial distribution of multiple species which direct their reproduction rates on one stand when the classical modelling (either mathematical or Markovian) cannot do so easily. Inversely, the multiple reiterations imposed by the random processes, the multiple replications, as well as the multiple sweeping of large arrays, yield the method time-expensive and harden the combinational exploration of the initial parameters. However the increase in computer power is already eliminating most of the limitations.

Lastly, the random simulation might bring help in understanding succession dynamics. The display of stationary and excitation phases, the subsequent settlement by steps of trees and the emergence of mosaic structures in the Callunadominated heathlands, constitute some results that could be some starting points for new researches in the fields of vegetation dynamics. Nevertheless, as it has been demonstrated by numerous authors the ecosystems are able to converge to different attractors such as multiple equilibriums (May, 1977; Gatto and Rinaldi, 1987), cyclical or chaotic ones (May and Oster, 1976; Deneubourg, 1977; Pacala and Silander, 1985; Pakes and Maller, 1990; Rinaldi and Muratori, 1992,1993). This complex behaviour, strongly dependent on and highly sensitive to the initial values of the parameters, added to the inherent random characteristics of certain parameters of the ecosystems (individual variations of the genotypes, climatic parameters, etc.) does not allow us to expect any long-term and accurate forecasting in the domain of terrestrial ecology.

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