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Dynamics of *Vaccinium myrtillus* patches in mountain spruce forest

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Abstract. The dynamics of *Vaccinium myrtillus* (bilberry) patches were studied in spruce (*Picea abies*) forest at the higher montane and lower subalpine level in the Tarentaise valley (Savoy, France). Although aerial parts of the shrub may give some indication of age and density of the patches, the annual growth and death of rhizomes are better indicators of patch dynamics. In some cases, dead and young rhizomes may occur simultaneously in the same patch, indicating that growth and death proceed continuously on the inside of dense patches. At mountain sites, slope position of plants significantly influences rhizome growth. A theoretical model of growth of bilberry patches is proposed which takes into account the anisotropic influence of slope and the postulated independence of different rhizome units belonging to the same individual.

Keywords: Bilberry-spruce forest; Heath; Humus; *Picea abies*; Synchronical analysis; *Vaccinio-Piceetea*.

Abbreviations: MB = Macot Bas; MH = Macot Haut.

Nomenclature: Rameau et al. (1993).

Introduction

Regeneration failure in mountain spruce forests, both at the higher montane and subalpine level have been noticed for a long time (see André et al. 1990; Ponge et al. 1994). This failure may be associated with the excessive development of ground vegetation. Bilberry-spruce forests are widespread in the Northern Alps, mainly on north exposures. In these forests, patches of *Vaccinium myrtillus* (bilberry) occur in the ground layer (Trepp 1961; André & Gensac 1989) and the forest may be considered a mosaic of developmental phases of spruce stands and patches of bilberry (Bernier & Ponge 1994; Ponge et al. 1994). A raw humus profile is built up under the bilberry which renders the soil conditions unfavourable for the establishment of spruce seedlings, irrespective of the light conditions (Bernier & Ponge 1994). Despite their abundance, bilberry patches in managed forests have not been well-described, although they are well-known as parts of heath ecosystems (e.g. Schaminée et al. 1993). In fact, the antagonism between forest bilberry heath and spruce fits the ‘inhibition model’ of Connell & Slatyer (1977), and also observations by Handley (1963) and Robinson (1971) on *Calluna* heath.

The growth of individuals of *Vaccinium myrtillus* has been studied by Flower-Ellis (1971). From the top of each rhizome several aerial and subterranean stems arise according to a sympodial pattern. Growth of the shoots is linear. The ramification of the rhizome system is achieved by reiteration of the following pattern: rhizomes may grow over long distances, at least 0.5 m, and for a very long time without ramifying, but they may suddenly shorten their internodes and diverge into several shoots and rhizomes (tillering). Shoots and rhizomes age and die locally during the development of each individual, thus fragmenting it. Gradually, the population becomes denser and increases in size, provided no antagonism takes place, for instance with a tree, and in the absence of environmental disturbances. The present study aims at (1) finding variables most useful to characterize phases of patch dynamics (van der Maarel 1988) of *Vaccinium myrtillus* in the absence of antagonisms, and (2) evaluating the influence of slope on the growth of these patches in mountain conditions. This paper is the first of a series which will deal with boundary types (van der Maarel 1990) of bilberry patches.

Material and Methods

Two bilberry-spruce forest (*Vaccinio-Piceetea*) stands were chosen on north-facing slopes (20–40 %) in the Macot La Plagne forest (Tarentaise Valley, Savoy, France), at two elevations. Vegetation, climate and soil

conditions were described by André et al. (1990) and humus profiles and soil fauna by Bernier et al. (1993). A high-montane site, Macot-Bas (MB), was chosen at 1650 m on a shale colluvium; and a lower subalpine site, Macot Haut (MH), at 1850 m on a quartzite colluvium. See André & Gensac (1989) for a morphological description of bilberry in these two sites. In the MB site the understory vegetation was made of patches of a dense bilberry heath (470 aerial shoots/m²), alternating with moss or herb patches, the heath covering about half of the total surface. Shoots were, on average, 24.5 cm long and 2.85 mm wide at their base. In the MH site the patches were more continuous, covering ca. 80 % of the surface, but less dense (180 aerial shoots/m²). The average length of shoots was 38.5 cm and their width at the base 3.5 mm. Productivity and regrowth after cutting were more important in MB than in MH (André & Gensac 1989), which can be understood as a difference in age (Miller & Miles 1970). Indices such as the diameter of the largest rhizomes or shoots (Flower-Ellis 1971) indicated that the bilberry heath was younger in MB. Thus we assumed that differences between MB and MH were not only due to altitude but also to the age of the bilberry.

Several types of bilberry patches were recognized in each site (F. Viel unpubl. 1988; Vuillermet unpubl. 1990), which were taken as a basis for the choice of our study plots. In the MB site, we compared a colonization zone A (herbaceous vegetation with sparse young bilberry shoots), a medium-density bilberry heath B, and a high-density bilberry heath C, with three replicates in each of them (Fig. 1). The vegetation in A consisted mainly of *Deschampsia flexuosa*, *Luzula sylvatica* and *Prenanthes purpurea*. In the MH site, we compared a zone of dense heath D, and a small area E within the bilberry heath where shoots were practically dead and the living vegetation was mainly *Luzula sylvatica*, again with three replicates (Fig. 1).

In each replicate a 50 cm x 50 cm plot was analyzed in July 1993 and 1994, both for aerial and subterranean parts of bilberry. The soil was excavated down to 10 cm, including the whole below-ground system of bilberry. Some measurements were made in the field, others were made on a map of the rhizome network (Fig. 2). The 10 larger shoot and rhizome diameters were measured, as well as total length and biomass of the below-ground system, separating increments of the current year (white rhizomes) from older ones (red rhizomes). Length and mass of white rhizomes were expressed as % total rhizome, and subterranean (white) apices as % total (subterranean and aerial) apex number. The age of 10 larger shoots was estimated by counting annual increments.

The five sites were compared by means of a one-way ANOVA with three replicates for each modality (Sokal & Rohlf 1969). The influence of slope on the growth of rhizome units (fixed arbitrarily at 10cm), taking

into account their age, was studied by means of a two-way ANOVA (slope and age, each with two modalities) with the 15 plots as blocks. Rhizome units falling within each of the four categories thus defined were counted. For analyzing the effects of slope and age, the units were counted as growing in the direction of the slope or against it, and as growing (current year) or standing (one year and more) respectively. The distribution of data residues of each ANOVA run was tested for normality (Sokal & Rohlf 1969). The threshold for rejection of the null hypothesis (absence of any effect) was 0.05. In each type of bilberry patch a humus profile was cut with a sharp knife and the thickness of three horizons (distinguished according to Anon. 1992) was measured.

Results

Both total length, biomass and mean diameter of 10 wider rhizome units were highest in D (Table 1). All plots except E showed white rhizomes. Dead rhizome parts were found in plots B and D, and especially E. Some variables did not follow the same trend. Active growth of below-ground parts, as deduced from the ratio biomass or length of growing parts to total biomass or length was found in B. Unexpectedly, some dead rhizomes were found in this medium-density heath zone. Thus, site B zone showed both youth (intense growth) and ageing (large diameters, decaying parts) features.

The decrease in subterranean parts observed in E, with a large percentage of dead rhizomes and the absence of growth (Table 1), fitted well with the idea that this zone represented a senescent bilberry heath.

As to the orientation of growing and standing parts of the rhizome system, there was a strong preference for growing down-slope (Table 2). This effect was much more prominent in standing parts, as indicated by the positive interaction age x slope. Thus, cessation of growth occurred probably in the course of time when rhizomes grew up-slope.

We observed a maximum density of aerial parts in C and a maximum biomass in D (Table 3). This discrepancy can be explained by a higher mean age (and thickness) of shoots in D. The decrease in aerial parts in E was more pronounced than for rhizomes (Table 1). The aerial/subterranean biomass ratio exhibited a decrease from A to E. The maximum thickness of the third humus horizon was reached in E; it was absent in A and B (Fig. 3). The second humus horizon was nearly absent in C and maximal in D (where also the thickest first horizon was found). This horizon was less variable. Thus the appearance of a thick third horizon is associated with a dense bilberry vegetation (C and D), with a maximum development in E where bilberry had died. The

humus profile in the colonization zone (A) and in the medium-density bilberry heath (B) was different from that under high-density (C and D) and died-off bilberry heath (E). Its features were typical of humus profiles developed under herbaceous vegetation as described by Bernier et al. (1993) and Bernier & Ponge (1994) in similar sites of the Macot forest.

Discussion

Vaccinium myrtillus, contrary to other ericaceous species, is characterized by its deciduous foliage and by a strong development of below-ground parts. It may develop clonal patches of a huge size (Billings & Mooney 1968). As a consequence, the genetic individual or genet is difficult to identify, like in other rhizomatous forest plant species (Antos & Zobel 1984). According to Flower-Ellis (1971) a rhizome may extend over a long distance, at least 5 m. Fragmentation is also commonly observed during patch development. This makes it impossible to identify patches as individuals (Keatinge 1975), as was done with *Calluna vulgaris* (Watt 1955) and *Rhododendron ferrugineum* (Pornon 1994) which grow by layering of aerial parts and thus may mechanically interfere with other individuals, giving a territory to each individual.

Flower-Ellis (1971) demonstrated that (1) individual growth was centrifugal, thus a colonization zone was present around each bilberry patch; (2) increasing density occurred in internal parts of the clone. Transect lines from the margin to the centre of a patch revealed developmental phases corresponding to two different kinds of occupation strategies (according to Flower- Ellis), namely (1) a youth phase, with a low density of aerial and subterranean parts and with a low diameter of shoots and rhizomes, (2) an adult phase with increasing density of both aerial and subterranean parts. No senescent phase was described by him, probably as a result of the recent establishment of bilberry in the sites he had to choose in order to avoid the coalescence of different individuals.

If we try to describe our plots in terms of youth, maturity and senescence according to Flower-Ellis (1971), it appears that the order A-B-C-D-E may be considered as following a sequence from colonization (A) to youth (B), to an adult stage (C followed by D) and at last to senescence (E). However, some deviations of this pattern were found. The B zone, which should be intermediate between the dense heath (C and D) and the colonization zone A, showed a number of dead rhizomes and of rhizomes and shoots of a large diameter, associated with a large number of growing rhizomes (Tables 1, 3). This was indicative of a more advanced state

than the denser plot C, although growth seemed to be more active in plot B. Knowledge of the sites from previous studies (André & Gensac 1989; André et al. 1990; Bernier et al. 1993) allowed us to explain some of these features. The MB site, where plots A, B and C had been chosen, suffered storms, a number of spruce trees being windthrown or windbroken (remaining stumps still visible, Fig. 1). Thus gaps occurred in the canopy. In some of these gaps *V. myrtillus* was previously absent (bilberry is absent or reduced under tree crowns), and hence was now in a state of colonization (Zone A). In some others bilberry was present but not thriving (Zone B) because of the antagonism of *Picea abies* (shading or other factors); this effect disappeared after storm felling. Thus the development of the bilberry heath did not seem to be a function of age only, but also of antagonistic effects such as the presence and development of tree crowns, and death of the trees. It should also be noticed that colonization of a site by bilberry (zone A) takes place in another, mainly herbaceous type of vegetation, with *Deschampsia flexuosa*, *Luzula sylvatica* and *Prenanthes purpurea*, where some antagonism may be expected too. These two points will be the subject of further studies.

The size of gaps, together with the presence or absence of bilberry prior to the death of the trees, may determine (1) whether an ericaceous or herbaceous vegetation will invade these openings, (2) what kind of humus profile will be built-up (Bernier & Ponge 1994) and (3) whether regeneration will occur or not (Ponge et al. 1994). In C, the gap between the trees was of a small size (2.5 m between adult trees). It had been invaded by a dense bilberry heath with a raw humus (Fig. 1). In A, this gap was larger (more than 10 m between the present adult trees). It had been invaded by a herbaceous vegetation and spruce seedlings with a mull humus (Fig. 1). The case of C, when compared with B, might indicate that the thickness of the raw humus layer depends more on density of the heath than on its age. In the case of the MH site, the D and E zones corresponded to an older bilberry heath, with widely extending rhizomes and shoots and decaying parts, but growth still seemed active in D, contrary to E where it had stopped.

The only process which could be described with certainty is the growth of rhizomes. From our observations a hypothetical model of development of bilberry patches may be built (Fig. 4). Colonization and increasing density and the centrifugal development of bilberry patches may be considered as the result of stochastic processes at the scale of the growing rhizome parts. In this model the driving process is the development of small-sized functional units (rhizomes + shoots) which we assumed to be independent of each other. This implies that the development of a functional unit is neither stimulated nor impeded by other units, and that its growth is the same whatever its position in the patch. In this case, following our model, the fact that a patch is made of a single or of several individuals is not important; it depends only on time and presence or

absence of antagonistic effects. Tillering is associated with the appearance, at a given point, of several shoots and one or more growing rhizomes (Fig. 2). A group of related shoots and rhizomes, issued from the same point, may be seen as a functional unit, without any relationship between this unit and the similar unit from which it has grown. In this case any experimental disruption of a standing rhizome should have no effect on the future development of actual shoots and growing rhizomes; the same should be true if a group of associated shoots and rhizomes were suppressed. This hypothetical process is similar to what happens during the development of the root system of trees (Bråkenhielm & Persson 1980; Persson 1980a, b, 1981, 1984).

The influence of the slope on the growth of rhizomes (statistically translated by the elliptical shape of a theoretical individual) may be considered as the above-mentioned process taking place in an anisotropic medium such as in diffusion processes (Crank 1956). The preferential down-slope growth of bilberry may be the mechanism by which changes in altitudinal localization of bilberry-spruce forests occur, as favoured by man opening the spruce forest (Bernier & Ponge 1993, 1994). The fact that the bilberry heath in MH seemed to be at a later stage of development than in MB may be considered as the result of this sliding effect. People living in Macot village remember that bilberry was previously absent at the montane level but that it appeared in zones opened by state foresters. The exact nature of this phenomenon is unknown, but it demonstrates that processes taking place in the humus profile at the scale of a few cm, may explain, when reiterated on large surfaces by the development of vegetation patches, changes in the landscape. Here, the influence of man is evident, in that (undesired) biological mechanisms are amplified. It could be put as a hypothesis for future studies that there is a natural tendency for rhizomes to grow more or less horizontally and that pure mineral soil hampers apex growth. When, by chance, a new rhizome grows up-slope it more rapidly encounters unfavourable conditions. This may also explain the observation that in a mor humus young rhizomes were more superficial than older ones (Heath et al. 1938); this process is at the origin of the development of the raw humus layer.

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Legends of figures

Fig. 1. Map of the Macot Bas and Macot Haut study areas, with the position of sampling plots, trees and tree stumps.

Fig. 2. Map of the rhizome system in plot B1.

Fig. 3. Thickness of organic horizons in one plot of each type of bilberry patch.

Fig. 4. Hypothetical development of a *Vaccinium myrtillus* patch in the absence of interference from spruce trees.

Table 1. Variables describing growth and standing crop (living + dead parts) of the below-ground parts of *Vaccinium myrtillus* in the five studied plots (means of three replicates). Plots belonging to the same group (Newman-Keuls test) share a common letter.

Plot	A	B	C	D	E	F-ratio	P
Total biomass (g/m ²)	16.0 b	111.3 ab	567.3 ab	660.3 a	197.0 ab	7.7	0.005 **
Total length (m/m ²)	11.0 d	34.9 bc	53.2 ab	60.1 a	20.2 cd	12.1	<0.001***
Mean diameter of 10 wider rhizome units(mm)	2.4 c	3.8 bc	4.5 bc	8.0 a	6.0 ab	6.9	0.007 **
Dead length (%)	0.0 b	3.1 b	0.0 b	6.5 b	17.2 a	17.3	0.001***
Growing length (%)	20.4	18.8	13.4	10.9	0.0	2.1	0.159 N.S
Growing dry weight(%)	12.9 a	3.1 b	1.5 b	1.0 b	0.0 b	24.6	<0.001***
Growing white parts / total number of apices (%)	44.7 a	31.3 a	28.0 a	16.6 a	0.0 b	16.2	<0.001***

Table 2. Analysis of variance of the influence of age and slope on the number of rhizome units (RU) of *Vaccinium myrtillus*, and of the interaction age x slope; DF = degrees of freedom.

Effects	DF	<i>F</i>	<i>P</i>
Age	1	41.6	<0.001***
Slope	1	31.8	<0.001***
Interaction Age x Slope	1	16.1	<0.001***
Interaction	Growing	Standing	
Downslope growth	5.0 RU	24.3 RU	
Upslope growth	2.0 RU	6.5 U	

Table 3. Variables describing standing crop and density of bilberry shoots in the five studied plots (means of three replicates). Plots belonging to the same group (Newman-Keuls test) are indicated by a common letter. N.S. = not significant.

Plot	A	B	C	D	E	<i>F</i> -ratio	<i>P</i>
Total biomass (g/m ²)	16.0 b	11 1.3 ab	567.3 ab	660.3 a	197.0 ab	7.7	0.005 **
Standing crop (living + dead) (g/m ²)	23.0 b	80.3 b	394.7 a	402.7 a	13.7 b	4.8	0.02 *
Shoot density (/m ²)	33.3 b	118.7 ab	212.0 a	161.3 a	24.0 b	10.5	0.002 **
Mean diameter of 10 wider shoots (mm)	2.2	2.9	3.9	4.8	3.4	1.9	0.196 N.S.
Mean age of shoots (yr)	3.0	3.3	4.0	4.3	2.2	2.4	0.122 N.S.
Aerial/subterranean biomass ratio	142.8 a	73.4 b	69.0 b	68.6 b	12.3 c	15.5	<0.001 ***

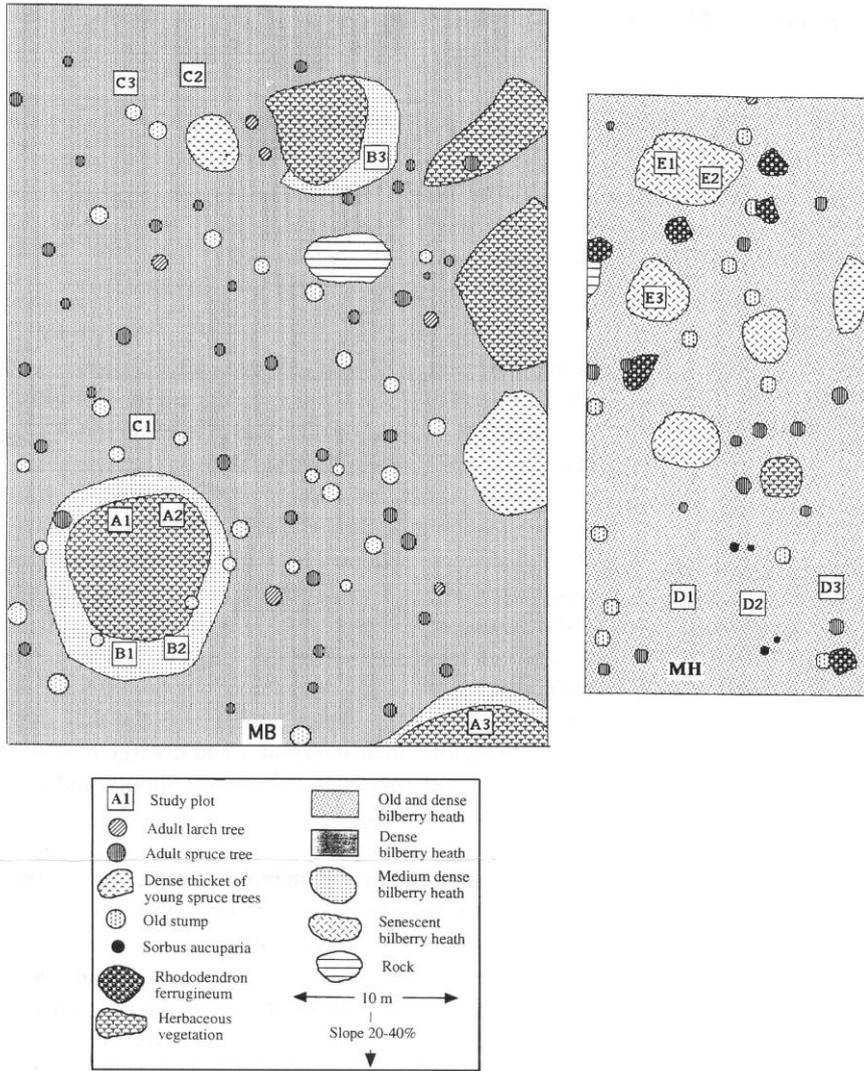


Fig. 1

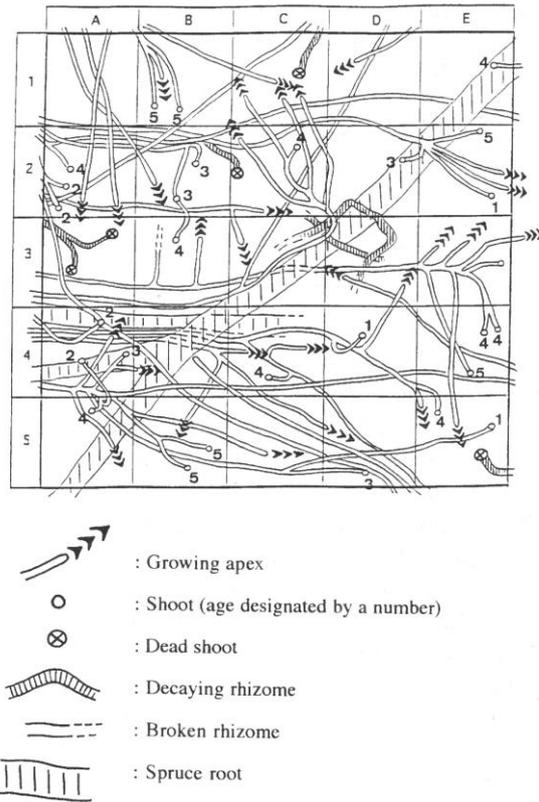


Fig. 2

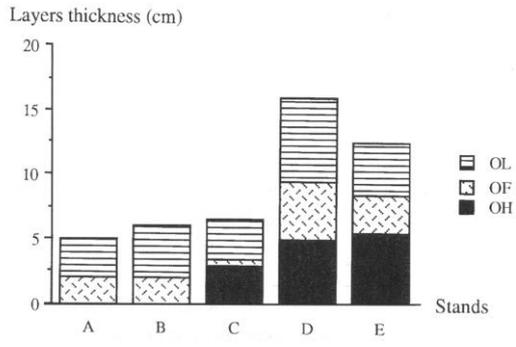


Fig. 3

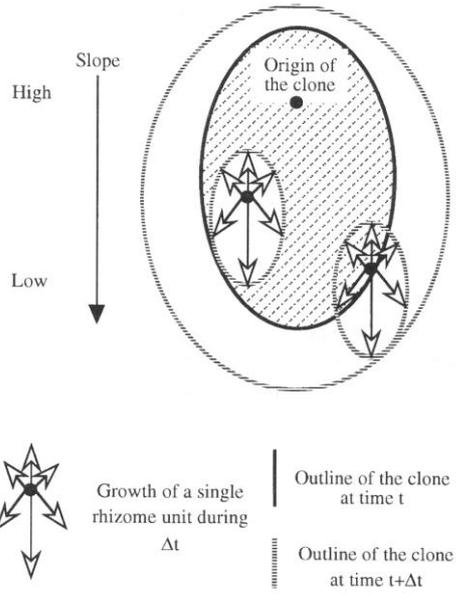


Fig. 4