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CLONAL DIVERSITY AND GENETIC STRUCTURE IN *VACCINIUM MYRTILLUS* POPULATIONS FROM DIFFERENT HABITATS

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ABSTRACT. — The life history traits of a clonal plant species, such as growth form and seedling recruitment pattern, influence the clonal diversity and structure within populations. Using Random Amplified Polymorphic DNA markers, we investigated the variation in clonal diversity and in spatial structure of clones in *Vaccinium myrtillus* populations from different habitats (mineral heath, peaty heath and beech grove). The partitioning of the genetic variability within and between populations was also studied. A total of 95 clones were identified among the 586 samples analysed. Despite an intra-population variability in the clonal diversity and in spatial structure of clones, no difference was detected between the different studied habitats. Although there was some variation in growth strategy, *V. myrtillus* exhibited a more typical phalanx growth form. Our results supported the hypothesis that the "recruitment at windows of opportunity" (RWO) is the most appropriate description of seedling recruitment in this species. In accordance with the life history traits of *V. myrtillus* (long-lived species with a mixed breeding system and potentially high seed dispersal), a high proportion of the genetic variation was observed within populations (86%) and only a low proportion of the genetic variation was distributed between populations (14%).

KEY WORDS. — Clonal structure, clonal growth form, seedling recruitment, genetic diversity, Ericaceae.

INTRODUCTION

Vegetative or clonal propagation is a characteristic of many plant species (COOK 1983). The growth form of a clonal plant species can greatly influence the level of diversity and the spatial distribution of clones within populations. Most clonal species have a growth form that falls between two extreme types, termed phalanx and guerilla (LOVETT DOUST 1981). In the phalanx growth form, clones produce short internodes leading to an advancing front of closely packed ramets. In the guerilla growth form, clones produce long internodes leading to an advancing front of widely spaced ramets. In phalanx species clones tend to form distinct clumps whereas clones of guerilla species are more likely to intermingle. However, the number and spatial structure of

clones may also be influenced by seedling recruitment patterns. Eriksson (1989, 1993) suggested that seedling recruitment patterns could range from repeated seedling recruitment (RSR) to initial seedling recruitment (ISR). When a species is characterised by an ISR pattern, seedlings are established during one period, with no further recruitment. In this case, populations are expected to consist of a few large clones. On the contrary, repeated seedling recruitment following the establishment of a population characterises the RSR pattern. Under this type of recruitment regime, populations are expected to consist of many small clones. Jelinski & Cheliak (1992) proposed a third intermediate scenario, called "recruitment at windows of opportunity" (RWO ; see also Eriksson & Froborg 1996). In the RWO model, the recruitment within stands of established conspecific adults is limited spatially and temporally. So, the seedling recruitment in the RWO pattern is similar but more occasional than in the RSR pattern (Eriksson & Froborg 1996).

Vaccinium myrtillus L. (Ericaceae) is a deciduous and rhizomatous shrub growing in a variety of temperate woodlands and heaths throughout Europe. Flower-Ellis (1971) studied *V. myrtillus* populations situated in forests in central Sweden and estimated the age of the oldest *V. myrtillus* clone at approximately 100 years. Therefore, *V. myrtillus* can be regarded as a long-lived species. It reproduces sexually and produces berries (Ritchie 1956). With an outcrossing rate ranging from 0.66 to 0.75 (Jacquemart *et al.* 1994), *V. myrtillus* is considered to be a mixed-mating species (Jacquemart & Thompson 1996, Jacquemart 2003). High dispersal capacity of *V. myrtillus* seeds, such as that by birds, is likely (Flower-Ellis 1971). Indeed, Flower-Ellis (1971) observed that seedling occurrence in nature often seems to be associated with bird droppings.

The first aim of this study was to investigate the variation in clonal diversity and spatial structure of clones in *V. myrtillus* populations from different habitats (mineral heath, peaty heath and beech grove) in a same geographical region. The second aim of this study was to estimate the partitioning of the genetic variability within and between populations in relation to the life history traits of this species. Indeed, the life history traits of a species (e.g., life form, breeding system, seed-dispersal strategy) can significantly influence the level and the distribution of genetic variability (Hamrick & Godt 1996, Bartish *et al.* 1999, Nybom & Bartish 2000).

MATERIAL AND METHODS

Study sites and sampling procedure

Six natural *V. myrtillus* populations were selected in three different habitats on the Plateau des Tailles in Upper Ardenne, Belgium. First, we sampled two mineral heath populations: 'Fayi de la Folie' (lat. N 50°15'04'', long. E 5°41'39'', alt. 550 m) and 'Minières d'Ottré' (lat. N 50°15'04'', long. E 5°50'28'', alt. 560 m). Second, we sampled two peaty heath populations: 'Robiefa' (lat. N 50°15'27'', long ; E 5°42'04'', alt. 570 m) and 'Sacrawé' (lat. N 50°15'00'', long. E 5°44'22'', alt. 652 m). Finally, we sampled two beech grove populations: 'Parc à Gibier' (lat. N 50°12'33''N, long. E 5°35'41'', alt. 450 m) and 'Le Poteau'(lat. N 50°13'34'', long. E 5°40'45'', alt. 600 m). The spatial distance among these populations ranged from 1 to 17 km. The 'Fayi de la Folie' population was characterised by a mixture of *V. myrtillus* (cover: 90%), *Calluna vulgaris*, *Deschampsia flexuosa* and was overgrown with *Pteridium aquilinum*. Some trees were present, including *Fagus sylvatica*, *Picea abies* and *Sorbus aucuparia*. A mixture of *V. myrtillus* (cover: 70%), *C. vulgaris*, *Vaccinium vitis-idaea* and *D. flexuosa* characterised the 'Minières d'Ottré' population. The 'Robiefa' population was characterised by a mixture of *Molinia caerulea*, *C. vulgaris*, *Vaccinium uliginosum*, *V. myrtillus* (cover: 10%), *Erica tetralix* and *V. vitis-idaea*. Only two tree species were present, *P. abies* and *S. aucuparia*. The 'Sacrawé' population was characterised by a mixture of *M. caerulea*, *C. vulgaris*, *V. myrtillus* (cover: 10%), *V. uliginosum*, *E. tetralix*, *Scirpus cespitosus* and *Vaccinium oxycoccos*. Several tree species were present in small numbers: *Pinus sylvestris*, *Salix* x *multinervis* and *Sorbus aucuparia*. A mixture of *F. sylvatica*, *Luzula luzuloides*, *D. flexuosa*, *Agrostis tenuis* and *V. myrtillus* (cover: 15%) characterised the 'Parc à Gibier' and the 'Le Poteau' populations. Some saplings of *S. aucuparia* and *P. abies* were also present. Based on a historical maps (map of the 'cabinet des Pays-Bas autrichiens', Ferraris, 1775 ; topographic map of Belgium, Vander

Maelen, 1853 ; topographic map of Belgium, Institut géographique militaire, 1924), the soil occupation of the study sites (heath or wood) has most likely not changed over the past two centuries. The 'Minières d'Ottré' population may be an exception due to disturbances caused by small-scale mining activities during the first half of the past century.

In each population, two 3 × 3 m sampling plots were selected in the middle of homogeneous patches of *V. myrtillus*. The spatial distance among plots within a population ranged from 4 to 120 m depending on the location of adequate patches. Within each plot, 49 twigs of *V. myrtillus* were collected at each point of intersection of a 0.5 × 0.5 m grid. In total, 588 samples were collected in April 1999. The young leaves were stored at –80°C until DNA extraction.

DNA isolation

DNA was extracted from young leaves using a modification of the CTAB procedure (Doyle & Doyle 1990). Details of the DNA extraction are given in Albert *et al.* (2003). The DNA concentration of each sample was estimated by fluorometry using bisbenzimidazol (Hoechst 33258 ; Labarca & Paigen 1980). DNA was quantified using a TKO100 Dedicated Mini Fluorometer (Hoefer Scientific Instruments) and samples were diluted to 5 ng μL^{-1} before amplification.

RAPD procedure

We used Random Amplified Polymorphic DNA (RAPD) markers to identify clones and to estimate the genetic variability within and between populations. In a previous study, we showed that RAPD markers and Amplified Fragment Length Polymorphism (AFLP) markers were equally effective in detecting clones in *V. myrtillus* (Albert *et al.* 2003). Given that we obtained identical clonal structures with both the RAPD and AFLP techniques, we chose RAPD for this study since it is a more cost- and time-effective marker .

PCR reactions were conducted in volumes of 25 µL containing 10 ng DNA, 2.5 µL 10× *Taq* buffer, 3 mM $MgCl_2$, 200 µM of each of the four dNTP's, 0.6 µM primer, 0.625 U *Taq* DNA polymerase (Roche) and 0.2 mg mL^{-1} BSA. PCR reactions were carried out in a GeneAmp PCR system 9700 DNA thermocycler (Perkin-Elmer). The programme began with an initial denaturation at 94°C for 4 min, followed by 35 cycles of 1 min at 94°C, 1 min at 36°C and 2 min at 72°C, and ended with 4 min at 72°C. PCR products were separated on 1.6% agarose gels (0.5X Tris-borate-EDTA buffer), run at 100 V for 195 min, stained with ethidium bromide and visualized under UV transillumination. The six primers used in this study were the same as those used in Albert *et al.* (2003). The presence or absence of DNA fragments were scored using the Molecular Analyst Software ver. 1.12 (Bio-Rad Laboratories 1994).

Data analyses

The genetic similarity was estimated between pairs of samples using the similarity index of Jaccard (Legendre & Legendre 1998) : $S_{xy} = n_{xy} / (n_x + n_y - n_{xy})$, where n_x is the number of bands in the sample x, n_y is the number of bands in the sample y, and n_{xy} is the number of common bands between samples x and y. A group of samples sharing the same genotype for all polymorphic loci was considered as belonging to the same clone.

To characterise genotypic diversity three indices were computed for each plot, following Ellstrand & Roose (1987) : (a) the number of clones, *G*, divided by the number of samples, *N* ; (b) Simpson's index corrected for finite sample size (Pielou 1969) : $D = 1 - [\Sigma\, n_i (n_i - 1) / N (N - 1)]$, where n_i is the number of samples of genotype i and *N* is the total number of samples. *D* ranges from 0 in a population composed of a single clone to 1 in a population where each sample has a unique genotype ss (Fager 1972): $E = (D_{obs} - D_{min}) / (D_{max} - D_{min})$, where $D_{min} = [(G - 1) (2N - G)] / [N (N - 1)]$ and $D_{max} = [N (G - 1)] / [G (N - 1)]$. E ranges from 0 in a population where each sample has the same genotype, or where one genotype dominates and the other genotypes are represented by a single sample, to 1 in a population where all genotypes are represented by the same number of samples.

Analysis of molecular variance (AMOVA ; Excoffier *et al.* 1992) was performed to compute the molecular variance components at different hierarchical levels. The analysis was realised on a matrix of squared Euclidean distances among all genotypes using arlequin ver. 2.000 (Schneider *et al.* 2000).

RESULTS

From the six selected primers, 37 polymorphic markers were generated. A total of 95 genotypes or clones were identified among the 586 samples analysed (two samples failed to be extracted). The number of marker differences between clones ranged from 1 to 15.

The number of clones, *G*, divided by the number of samples, *N*, ranged from 0.06 to 0.43 in

TABLE 1

Genotypic diversity indicators in the six sampled Vaccinium myrtillus *populations on the Plateau des Tailles, Upper Ardenne, Belgium*

Habitat	Population name	Plot name	*N*	*G*	*G*/*N*	*D*	*E*
Mineral heath	Fayi de la Folie	MH1	49	7	0.14	0.58	0.54
		MH2	49	3	0.06	0.22	0.24
	Minières d'Ottré	MH3	49	3	0.06	0.19	0.18
		MH4	49	21	0.43	0.94	0.90
Peaty heath	Robiefa	PH1	49	14	0.29	0.79	0.68
		PH2	49	4	0.08	0.23	0.17
	Sacrawé	PH3	48	9	0.19	0.04	0.63
		PH4	49	2	0.04	0.79	0.00
Beech grove	Parc à Gibier	BG1	48	9	0.19	0.50	0.31
		BG2	49	8	0.16	0.33	0.11
	Le Poteau	BG3	49	14	0.29	0.86	0.82
		BG4	49	3	0.06	0.19	0.18

Note. *N* = number of samples, *G* = number of clones, *D* = Simpson's diversity index, *E* = genotypic evenness.

mineral heath populations, from 0.04 to 0.29 in peaty heath populations, and from 0.06 to 0.29 in beech grove populations (Table 1). The values of Simpson's index corrected for finite sample size, *D*, ranged from 0.19 to 0.94 in mineral heath populations, from 0.04 to 0.79 in peaty heath populations, and from 0.19 to 0.86 in beech grove populations (Table 1). The values of genotypic evenness, *E*, ranged from 0.18 to 0.90 in mineral heath populations, from 0 to 0.68 in peaty heath populations, and from 0.18 to 0.82 in beech grove populations (Table 1). These genotypic diversity indicators did not vary significantly among habitats (Kruskal-Wallis' tests, $P = 0.93$ for *G*/*N* ; $P = 0.99$ for D and $P = 0.94$ for E).

The number of clones per plot was highly variable, ranging from 2 to 21 (Table 1), with certain plots largely dominated by only one or a few clones (e.g., plots MH2, PH4 and BG4 ; see Fig. 1). In some instances, clones represented by only one ramet were isolated in the middle of bigger clones (clone 35 in PH1 plot, clones 48 and 49 in PH2 plot, clones 56 and 57 in PH3 plot, clone 64 in BG1 plot, and clone 72 in BG2 plot ; see Fig. 1). Generally, samples belonging to the same clone tended to be quite closely aggregated and to form distinct clumps (Fig. 1). However, some samples belonging to the same clone were loosely associated and clone intermingling occurred (clone 5 in MH1 plot ; clones 14, 17, 18, 20, 23 and 27 in MH4 plot ; clones 33, 34 and 41 in PH1 plot ; clones 63 and 69 in BG1 plot ; clone 73 in BG2 plot ; and clones 80, 83, 86 and 88 in BG3 plot ; see Fig. 1). None of the genotypes occurred in more than one population. However, two clones occurred in more than one plot within a population. Indeed, clones 3 and 5 both occurred in plots MH1 and MH2. These two plots were four metres apart and were situated in the same big patch of *V. myrtillus*.

Partitioning the variation within and between populations using AMOVA analysis showed that 13.81 % of the genetic variability existed as variation between populations and the remaining 86.19 % as variation within populations (Table 2).

DISCUSSION

CLONAL DIVERSITY AND STRUCTURE

The genotypic diversity indices (Table 1) indicate that the number and size of clones within plots were highly variable even within the same population. Because of the high within population variability, it was not surprising that these genotypic diversity indices did not vary significantly among habitats.

In a previous study of a single peaty heath population of *V. myrtillus*, we found that the

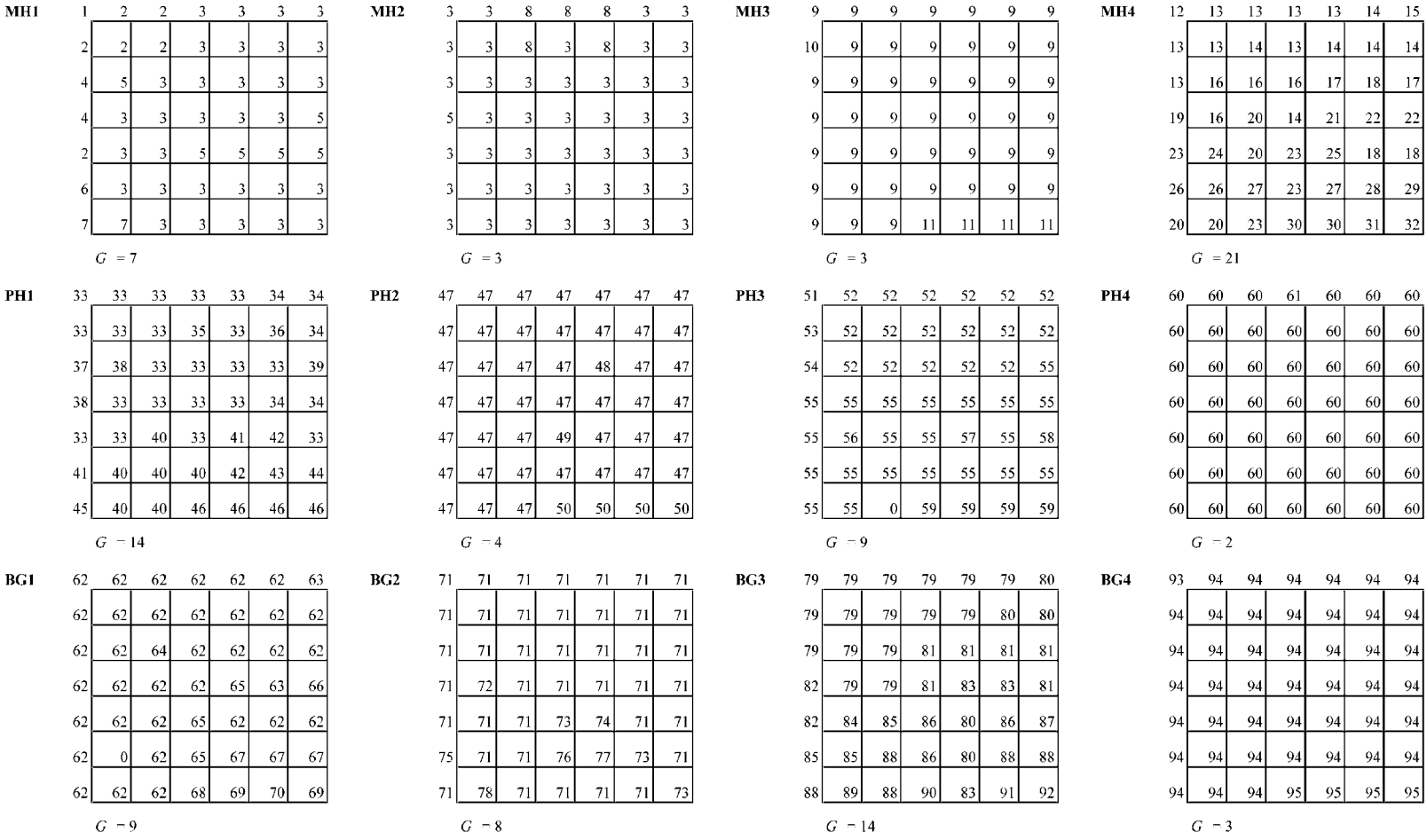

FIG. 1. — Spatial distribution of *Vaccinium myrtillus* clones in three habitats : mineral heath (MH1 to MH4), peaty heath (PH1 to PH4) and beech grove (BG1 to BG4). In each 3 X 3 m sampling plot, samples were collected at each point of intersection of a 0.5 X 0.5 m grid. Samples belonging to the same clone are represented by the same number. The absence of data is indicated by 0. *G* indicates the number of clones observed in a plot.

TABLE 2

Analysis of molecular variance (AMOVA) of RAPD data from six populations of Vaccinium myrtillus. *Levels of significance are based on 1000 permutations*

Source of variation	d.f.	Variance components	Percentage of variation	Probability
Among populations	5	0.56	13.81	$P < 0.00001$
Within populations	89	3.49	86.19	$P < 0.00001$

species exhibited a typical phalanx clonal growth form. In the present study, most of the clones also showed this growth form, i.e. ramets belonging to the same clone tended to be closely aggregated and those clones thus tended to form distinct clumps (LOVETT DOUST 1981 ; Fig. 1). In six plots, however, some ramets belonging to the same clone were loosely associated and clones were more intermingled (Fig. 1). This pattern is more typical of the guerilla growth strategy (LOVETT DOUST 1981). Despite this variation along the continuum between typical phalanx and guerilla growth strategies, *V. myrtillus* seems to be located closer to the phalanx end of the continuum. The observed variation in growth form resulted in an intra-population variability of the spatial structure of clones, but no difference was detected between the different studied habitats. Variation in clonal growth form was also observed in two other Ericaceae species, *Vaccinicum vitis-idaea* L. (PERSSON & GUSTAVSSON 2001) and *V. macrocarpon* Aiton (STEWART & NILSEN 1995), as well as in other plant species, e.g., *Ranunculus repens* L. (LOVETT DOUST 1981) and *Carex bigelowii* Torrey ex Schweinitz (JONSSON *et al.* 1996). Architectural parameters such as internode length and branching angle may respond plastically to environmental heterogeneity with significant consequences on the spatial structure of clones (MCLELLAN *et al.* 1997), which may explain intra- or inter-population variation in clonal structure. Therefore, although a species may be characterised as a whole as having a phalanx or a guerilla growth form, this does not mean that the growth form is a fixed trait.

ERIKSSON & FROBORG (1996) observed that in *V. myrtillus* the recruitment is limited by a combination of seed and microsite availability. Subsequently, these authors concluded that the "recruitment at windows of opportunity" (RWO), where recruitment within stands of established conspecific adults is limited spatially and temporally, is the most appropriate description of seedling recruitment in this species. The small clones isolated in the middle of bigger clones (Fig. 1) support this hypothesis. Indeed, it is likely that at least some of these small clones, which differed in only one band (clones 47 and 49, clones 55 and 56, clones 62 and 64) or a few bands (clones 33 and 35, clones 47 and 48, clones 55 and 57, differing in 4, 4 and 2 bands respectively) from the bigger surrounding clones, were offspring of the surrounding clones, suggesting that seedling recruitment occurred after the founding of the population. Although the clones that differed by only one band might be the result of somatic mutations, we do not believe that this was the case. Indeed a few additional bands, which were not selected for the analysis of the whole set of clones, differentiated these small clones from the bigger surrounding clones. The almost total absence of seedlings and the absence of a seed bank observed in *V. myrtillus*, despite a high production of well-dispersed seeds (VANDER KLOET & HILL 1994, JACQUEMART *et al.* 2003), can be understood in the context of RWO since occasional success at windows of opportunity favours features enhancing the ability of seeds to find these windows (ERIKSSON & FROBORG 1996).

Besides life history traits such as growth form and seedling recruitment pattern, several other factors, including the number of founding individuals, the age of the population and local ecological factors, can influence the local clonal diversity and spatial structure (HANGELBROECK *et*

al. 2002). Consequently, established clonal plant populations, even those in a similar habitat, might be expected to show unique patterns of clonal structure and diversity.

Partitioning of genetic variation

According to the AMOVA analysis, a high proportion of the genetic variation was observed within populations (86.19%) and only a low proportion of the genetic variation was distributed between populations (13.81% ; Table 2). In a study on *V. vitis-idaea* based on an AMOVA analysis of RAPD variation, Persson & Gustavsson (2001) also observed that the highest proportion of the genetic variability existed as variation within populations (89.20%). The partitioning of the genetic variability within and between populations observed in our study is comparable to that obtained in several RAPD-based AMOVA studies on woody and herbaceous species with a long-lived and outcrossing breeding system (see Bartish *et al.* 1999 for a review). Life history traits of species, in particular life form, breeding system and seed-dispersal strategy appear to be critical for explaining the level of genetic variability and its partitioning within and between populations (Hamrick & Godt 1996, Bartish *et al.* 1999, Nybom & Bartish 2000). *Vaccinium myrtillus* is a long-lived species with a mixed breeding system and potentially high seed dispersal (Flower-Ellis 1971, Jacquemart *et al.* 1994). The observed partitioning of genetic variation is in accordance with the species life history traits. Caution should be exercised, however, in generalising the results on the partitioning of the genetic variability to the species as a whole since, at a much greater geographic scale, genetic differentiation between populations (G_{ST}) is likely to increase due to a decrease in gene flow. This seemed to be the case in a previous isozyme study on the mating system and genetic structure in *V. myrtillus* (Jacquemart *et al.* 1994), in which higher G_{ST} values were observed at the European level as compared to the Belgian level.

To summarise, this study revealed an important intra-population variability in clonal diversity and spatial structure of clones in *V. myrtillus*, but no consistent difference was detected between the studied habitats. Although there was some variation in the growth strategy, *V. myrtillus* exhibited a more typical phalanx growth form. Our results support the hypothesis that the “recruitment at windows of opportunity” (RWO) is the most appropriate description of seedling recruitment in this species. In accordance with the life history traits of *V. myrtillus*, a high proportion of the genetic variation was found within populations while only a low proportion of the genetic variation was distributed between populations.

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REFERENCES

Albert T., Raspé O. & Jacquemart A. L., 2003. — Clonal structure in *Vaccinium myrtillus* L. revealed by RAPD and AFLP markers. *Int. J. Plant Sci.* **164** : 649-655.

Bartish I. V., Jeppsson N. & Nybom H., 1999. — Population genetic structure in the dioecious pioneer plant species *Hippophae rhamnoides* investigated by random amplified polymorphic DNA (RAPD) markers. *Mol. Ecol.* **8** : 791-802.

Bio-Rad Laboratories, 1994. — *Molecular snalyst software*, ver.1.12.

Cook R. E., 1983. — Clonal plant populations. *Amer. Sci.* **71** : 244-253.

Doyle J. J. & Doyle J. L., 1990. — Isolation of plant DNA from fresh tissue. *Focus* **12**: 13-15.

Ellstrand N. C. & Roose M. L., 1987. — Patterns of genotypic diversity in clonal plant species. *Amer. J. Bot.* **74** : 123-131.

Eriksson O., 1989. — Seedling dynamics and life histories in clonal plants. *Oikos* **55** : 231-238.

Eriksson O., 1993. — Dynamics of genets in clonal plants. *Trends Ecol. Evol.* **8** : 313-316.

ERIKSSON O. & FROBORG H., 1996. — "Windows of opportunity" for recruitment in long-lived clonal plants : experimental studies of seedling establishment in *Vaccinium* shrubs. *Can. J. Bot.* **74** : 1369-1374.

EXCOFFIER L., SMOUSE P. E. & QUATTRO J. M., 1992. — Analysis of molecular variance inferred from metric distances among DNA haplotypes : application to human mitochondrial DNA restriction data. *Genetics* **131** : 479-491.

FAGER E. W., 1972. — Diversity : a sampling study. *Amer. Nat.* **106** : 293-310.

FLOWER-ELLIS J. G. K., 1971. — Age structure and dynamics in stands of bilberry (*Vaccinium myrtillus* L.). *Avdelningen for Skoqsekologi Stockholm, Rapporter och Uppsatser* **9** : 1-108.

HAMRICK J. L. & GODT M. J. W., 1996. — Effects of life history traits on genetic diversity in plant species. *Phil. Trans. Roy. Soc. London Series B-Biol. Sci.* **351** : 1291-1298.

HANGELBROECK H. H., OUBORG N. J., SANTAMARIA L. & SCHWENK K., 2002. — Clonal diversity and structure within a population of the pondweed *Potamogeton pectinatus* foraged by Bewick's swans. *Mol. Ecol.* **11** : 2137-2150.

JACQUEMART A. L., 2003. — Floral traits of Belgian Ericaceae species : are they good indicators to assess the breeding systems ? *Belg. J. Bot.* **136** : 154-164.

JACQUEMART A. L. & THOMPSON J. D., 1996. — Floral and pollination biology of three sympatric *Vaccinium* (Ericaceae) species in the Upper Ardennes, Belgium. *Can. J. Bot.* **74** : 210-221.

JACQUEMART A. L., CHAMPLUVIER D. & DE SLOOVER J. R., 2003. — A test of mowing and soil-removal restoration techniques in wet heaths of the High Ardenne, Belgium. *Wetlands* **23** : 376-385.

JACQUEMART A. L., MAHY G., RASPÉ O. & DE SLOOVER J. R., 1994. — An isozyme study in bilberry (*Vaccinium myrtillus*). 2. Mating system and genetic structure. *Belg. J. Bot.* **127** : 105-114.

JELINSKI D. E. & CHELIAK W. M., 1992. — Genetic diversity and spatial subdivision of *Populus tremuloides* (Salicaceae) in a heterogeneous landscape. *Amer. J. Bot.* **79** : 728-736.

JONSSON B. O., JONSDOTTIR I. S. & CRONBERG N., 1996. — Clonal diversity and allozyme variation in populations of the arctic sedge *Carex bigelowii* (Cyperaceae). *J. Ecol.* **84** : 449-459.

LABARCA C. & PAIGEN K., 1980. — A simple, rapid, and sensitive DNA assay procedure. *Anal. Biochem.* **102** : 344-352.

LEGENDRE P. & LEGENDRE N., 1998. — *Numerical ecology* : 853 p. Elsevier Science, Amsterdam, The Netherlands.

LOVETT DOUST J., 1981. — Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*) I. The dynamics of ramets in contrasting habitats. *J. Ecol.* **69** : 743-755.

MCLELLAN A., PRATI D., KALTZ O. & SCHMID B., 1997. — Structure and analysis of phenotypic and genetic variation in clonal plants. *In* : DE KROON H. & VAN GROENENDAEL J. (eds.), *The ecology and evolution of clonal plants*, pp. 1-29. Backhuys Publishers, Leiden, The Netherlands.

NYBOM H. & BARTISH I. V., 2000. — Effects of life history traits and sampling strategies on genetic diversity estimates obtained with RAPD markers in plants. *Persp. Plant Ecol. Evol. Syst.* **3** : 93-114.

PERSSON H. A. & GUSTAVSSON B. A., 2001. — The extent of clonality and genetic diversity in lingonberry (*Vaccinium vitis-idaea* L.) revealed by RAPDs and leaf-shape analysis. *Mol. Ecol.* **10** : 1385-1397.

PIELOU E. C., 1969. — *An introduction to mathematical ecology* : 286 p. Wiley, New York.

RITCHIE J. C., 1956. — Biological Flora of the British Isles *:Vaccinium myrtillus* L. *J. Ecol.* **44** : 291-299.

SCHNEIDER S., ROESSLI D. & EXCOFFIER L., 2000. — ARLEQUIN : a software for population genetics data analysis, ver. 2.000. Genetics and Biometry Lab, Dept. of Anthropology, University of Geneva, Geneva, Switzerland.

STEWART C. N. & NILSEN E. T., 1995. — Phenotypic plasticity and genetic variation of *Vaccinium macrocarpon*, the American cranberry. II. Reaction norms and spatial clonal patterns in two marginal populations. *Int. J. Plant Sci.* **156** : 698-709.

VANDER KLOET S. P. & HILL N. M., 1994. — The paradox of berry production in temperate species of *Vaccinium*. *Can. J. Bot.* **72** : 52-58.