Gene frequency distributions of *Anthoxanthum alpinum* along the altitudinal gradients in Swiss Alps*

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Abstract : *Anthoxanthum alpinum* has a continuous distribution from the treeline (1700 m) to the summit ridges (2830 m) in Arpette and Belalp of Valais, Swiss Alps. The highest and lowest sites of the transect differ by almost 1000 m in elevation, but only an average of 1.4 km apart. A significant clinal variation was observed at three allozyme loci (*Px_1*, *Got_2* and *Mdh_1*) on all three transects. It suggests that gene flow among sub-populations may be too weak to overcome the effects of natural selection in favor of adaptations to local conditions, and that temperature variables may function as major selective force in this case.

Key words : *Anthoxanthum alpinum*, clinal variation, enzyme polymorphism, altitudinal gradient, alpine plant

Introduction

Numerous descriptions of genetic polymorphism illustrate that the patterns of genetic diversity are at least in part not random. Allele frequency clines at enzyme loci along ecogeographical gradients have been regularly found (Clegg and Allard, 1972; Hamrick and Allard, 1972; Bergmann, 1978; Bergmann and Gregorius, 1993; Nevo et al., 1979; Mitton et al., 1980; Kahler et al., 1980; Millar, 1983; Lumaret, 1984; Breitenbach-Dorfer et al., 1992). Allele frequency clines were considered to be important in speciation (Endler, 1977), and were explained by historical factors as postglacial migration in *Abies alba* (Breitenbach-Dorfer et al., 1992) and recent contact of formerly isolated populations of *Pinus muricata* (Millar, 1983). Allozymic variation in *Fagus sylvatica* showed to be related either to climate or to geography depending on the markers used (Felber and Thiebaut, 1984; Cuguen et al., 1985). Action of selection was also considered to be probable for explaining genetic differentiation among the populations of *Pinus ponderosa* along an altitude transect (Mitton et al., 1980) and *Picea abies* along similar climatic gradients (Bergmann, 1978).

We are involved, since 1993, in the project "Environmental Changes and Modification in the Sub-alpine-alpine Ecocline" launched by Swiss Priority Program ENVIRONMENT. The objective of the project is to follow the evolution of the transition zone between upper limit of the sub-alpine forest and treeless alpine zone, with the help of "phyto-indicator" of the modification and the genetics of indicative species.

Anthoxanthum alpinum Løve & Løve (Poaceae) is a widespread, perennial grass species in alpine regions, extending throughout the sub-alpine-alpine belts, ranging approximately from 1700 m to the highest ridgetops at our study sites in Swiss Alps in Valais. At lower altitude, *A. alpinum* is replaced by a closely related species, *A. odoratum* (Felber, 1986). This broad distribution provides ideal opportunities to study genetic response of plant sub-populations to environmental changes, because some important environmental conditions change rapidly with altitude. These conditions often

influence opportunities for gene flow and selection (Waser ,1978 ;Galen and Kevan ,1980 ;Galen et al. ,1991).

The objective of the study is to investigate the variability of isozyme loci in *A. alpinum* populations in the sub_alpine_alpine transitions in order to seek genetic markers correlated with altitudinal gradients (space scale) that can be later used for monitoring genetic response to environment changes (time scale).

Materials and methods

Plant materials

A total of 18 diploid sub_populations of *A. alpinum* ($2n = 10$) were sampled over three transects on siliceous rocks in two different parts of Valais in the Swiss Alps. The first transect was located in Val d'Arpette , in the extreme eastern part of the Mont_Blanc massif. It was a narrow side valley , east-west oriented , located on the left side of the Rhone River , above Martigny. The second transect was located at Belalp , in the Aletsch region , in the southern part of the Aar massif. the region of Belalp is a wide open lateral valley , north_south oriented , on the right side of the Rhone River (Fig. 1).

Fig. 1 Two sample sites located in Swiss Alps

Sampling was always performed according to an interval altitude of 1700 ~ 1900 m , 1900 ~ 2100 m , 2100 ~ 2300 m , 2300 ~ 2500 m , 2500 ~ 2700 m , 2700 ~ 2900 m , depending on the distribution of the species in the location. In 1993 , nine sub_populations were collected on five sites on the transect of Arpette and four on the transect of Belalp , respectively. In 1994 , 4 other sub_populations were collected on the both transects to cover all altitudinal intervals. In addition , a secondary transect , five sub_populations , was performed in Belalp in order to test preliminary results. Each sub_population consisted of 50 ~ 80 individuals collected at a distance of at least one meter. The only exception is in Arpette , 2780 m , where only a few individuals were found. The plants collected were afterward cultivated in the experimental garden of the University of Neuchatel.

Electrophoresis

For the extraction of soluble proteins , fresh leaf tissue of plants cultivated in the experimental garden was collected and ground at 4°C in 500 ml extraction buffer (0.1 M Tris_HCL , pH 7.5 , 0.1 M

thioglycolate sodium ,0.7% (w/v) ,polyethyleneglycol 20 000). The crude homogenates were centrifuged at 1200 g for 20 minutes at 4℃ . The supernatants were collected and then stored at - 80℃ .

Electrophoresis was carried out on horizontal starch gels(12%) and on vertical polyacrylamide gels (9%). Histidine_citrate buffer system was used in the starch gels for electrophoresis separation of malate dehydrogenases (*Mdh*) , phosphogluconate dehydrogenases (*Pgd*) , peroxidases (*Px*) , and alcohol dehydrogenases (*Adh*)(electrode buffer : 0.065 M L_Histidine/0.007 M Citric acid , pH 6.5 ; gel buffer : 0.0162 M L_Histidine/0.00175 M Citric acid , pH 6.5 ; migration : 20 min at 25 mA/100V , 4h at 60 mA/300V and 2h at 40 mA/200V). *Px* migrating to the anode as well as migrating to the cathode was considered. Glycine_Trис buffer system was used for electrophoresis separation of glutamate oxaloacetate transaminases(*Got*) and tetrazolium oxydases(*To*) in the vertical polyacrylamide gels(electrode buffer : 0.1 M Glycine /0.007 M Tris , pH 8.6 ; migration : 3h at 160 mA/600V).

Table 1 Correlation analysis between allelic frequencies and altitudinal gradients

Alleles	N	R
<i>Adh_1a</i>	18	-0.200
<i>Adh_1b</i>	18	0.139
<i>Adh_1c</i>	18	-0.035
<i>Px_1a</i>	18	0.656 **
<i>Px_1b</i>	18	-0.656 **
<i>CPx_1a</i>	18	0.214
<i>CPx_1b</i>	18	0.214
<i>Got_1a</i>	18	-0.382
<i>Got_1b</i>	18	0.244
<i>Got_1c</i>	18	-0.001
<i>Got_1d</i>	18	0.222
<i>Got_1e</i>	18	-0.055
<i>Got_2a</i>	18	0.174
<i>Got_2b</i>	18	-0.392
<i>Got_2c</i>	18	0.321
<i>Got_2c</i>	15	0.673 **
<i>Mdh_1a</i>	18	-0.203
<i>Mdh_1b</i>	18	0.738 ***
<i>Mdh_1c</i>	18	-0.200
<i>Pgd_1a</i>	18	-0.215
<i>Pgd_1b</i>	18	0.347
<i>Pgd_1c</i>	18	-0.198
<i>Pgd_2a</i>	18	0.184
<i>Pgd_2b</i>	18	-0.150
<i>Pgd_2c</i>	18	-0.265
<i>To_1a</i>	18	0.131
<i>To_1b</i>	18	-0.131
<i>To_2a</i>	18	-0.162
<i>To_2b</i>	18	0.162

Note : * * = P < 0.01 ;
* * * = P < 0.001

Enzyme staining for *Mdh* , *Adh* and *Pgd* was performed according to the methods described by Wendel and Weeden (1989). *Px* was stained by the use of the method described by Lumaret (1982). *To* was stained with the methods described by Valero (1980). In general , substrate concentrations had to be adjusted in respect to the original methods.

Zymograms were analysed according to Zeroual _Humbert_Droz (1985). When one locus coded for several alleles , the slowest_migrating allele was designated as allele *a* , the others , in turn , were *b* , *c* , *d* up to *e* , according to the number of alleles.

Results

Six enzyme systems including 11 loci were tested in the study. Pearson correlation analysis showed that a significant correlation was found between allelic frequencies of *Got_2c* , *Px_1a* and *Mdh_1b* and altitudinal gradients in all three transects studied (Table 1).

The *Got* polymorphism found in *A. alpinum* was controlled by two gene loci. One of these loci (*Got_1*) , coding for the slower migrating *Got* zone in zymograms , exhibited five alleles in our study material , the other gene locus (*Got_2*) was found to exhibit three different allelic types. At *Got_2* locus , although allele *a* and *b* were statistically heterogeneous , the degree of differences from sub_population to sub_population was small. Allele *c* increased with elevations in frequency from 0.086 to 0.135 and 0.087 to 0.189 on two transects in Belalp_1 and Belalp_2 , respectively. However , the situation was very complicated on the transect in Arpette where frequencies of allele *c* in the sub_population 2215 m and crest sub_

populations , i. e. at 2620 m and 2780 m were very low (Fig. 2). In order to verify this preliminary result , a secondary sub_population (at 2200 m) was sampled in Arpette in 1994 , and a similar result was obtained (Fig. 2). The result indicates that there was different genetic response to micro-habitat conditions at *Got_2* locus. Furthermore , it is worthy to note that the allelic frequencies of *Got_2c* tended to decrease in crest sub_populations in two localities. This may be due to environmental pressure encountered in the crest sub_populations more than in the other ones. When 15 sub_populations (except for three crest sub_populations) were pooled , a significant correlation ($R = 0.67$, $P = 0.006$) between allele frequencies and altitude was obtained (Table 1). χ^2 tests for deviation from Hardy_Weinberg expectation at *Got_2* were not significant except for the sub_populations in Arpette 2415 m and Belalp_2 2550 m where a significant deficiency of heterozygotes was found , while the lower sub_populations at Arpette (1830 m , 2015m and 2200 a) and at Belalp_2 (1815 m and 2030 m) and the higher sub_populations at Belalp_1 (2575 m and 2830 m) showed no significant excess of heterozygotes (Table 2).

Table 2 Fixation indices for each transect

Populations	<i>Px_1</i>	<i>Got_2</i>
<i>Arpette</i>		
1830	0.518 *	- 0.086
2015	0.541	- 0.100
2200_a	0.330 *	- 0.032
2200_b	0.564	0.112
2415	0.441 *	0.190 *
2445	0.443 *	0.164
2620	0.370 *	0.104
2780	0.249	- 0.133
<i>Belalp_1</i>		
2020	0.553	0.206
2200	0.593	0.189
2405	0.727	0.046
2575	0.332 *	- 0.081
2830	0.161	- 0.169
<i>Belalp_2</i>		
1815	0.478	- 0.100
2030	0.753	- 0.098
2230	0.406 * *	0.042
2430	0.217 *	0.033
2550	0.363	0.260 *

* = $P < 0.05$, * * = $P < 0.01$.

Anode peroxidase (*Px_1*) , coding for the slower migrating *Px* zone in zymograms , exhibited only two alleles. A gradual allelic frequency changed along altitude gradients was observed on all three transects ($R = 0.66$, $P = 0.003$) , although some differences existed in three transects (Fig. 3). χ^2 tests for deviation from Hardy_Weinberg expectation at *Px_1* showed that almost half of values showed a significant deficiency of heterozygotes (Table 2). This may suggest that there were directional selection for these two alleles at *Px_1* locus in two localities.

Mdh_1 , coding for the slower migrating *Mdh* zone in zymograms , exhibited three alleles and was highly polymorphic. Hybrid bands were often expressed either between allele *a* and *b* , or between allele *b* and *c*. Based on altitude , gene frequency of allele *b* increased with elevations on the three transects and showed a significant correlation with altitude ($R = 0.74$, $P = 0.0005$) when 18 sub_populations were pooled (Table 1 and Fig. 4).

Discussion

Geographical variation of morphological and allozyme characters in plant populations has been observed in many species (Clausen et al. , 1940 ; Grant and Hunter , 1962 ; Ward , 1969 ; Rochow , 1970 ; Hamrick and allard , 1972 ; Schaal , 1975 ; Davies and Snaydon , 1976 ; Snaydon and Davies , 1976 ; Waser , 1978 ; Silander , 1979 ; Silander and Antonovics , 1979 ; Chapin and Chapin , 1981 ; Linhart et al. , 1981 ; Meinzer et al. , 1985 ; Waser and Price , 1985 ; Galen et al. , 1991). Allele frequency clines at enzyme loci associated with environmental variables suggest that variation may be maintained by natural selection. Bergmannn (1978) found correlation between allele frequencies at acid phosphatase(*AcpH*) locus and climatic patterns along latitudinal and altitudinal gradients in *Picea*

abies. Similar clines were also detected at phosphoglucumutase (*Pgm*) locus along a steep elevation-al transect in *Pinus ponderosa* (Mitton et al. , 1980). Functional differences between allozymes (Breitenbach_Dorfer et al. , 1992) as well as a correlation between temperature

Fig.2 Distribution of allelic frequency of *Got-2c* along three altitude transects

Fig.3 Distribution of allelic frequency of *Px-1a* along three altitude transects

Fig.4 Distribution of allelic frequency of *Mdh-1b* along three altitude transects

gradient and thermostability of allozymes (Bergmann and Gregorius , 1993) at *Idh_2* locus in *Abies alba* populations furtherly indicated the role of selection. In contrast , Baker et al. , (1975) and Schaal and Smith (1980) found no significant variation in allozyme frequencies among sub_populations of *Silene maritima* and low levels of sub_population heterogeneity in *Desmodium nudiflorum* , respectively. Similarly , Oyama et al. , (1993) also reported low levels of genetic variation at allozyme loci among *Arabis serrata* sub_populations along an altitudinal gradient in Fuji Mountain in Japan , despite a great variation in morphological and ecological traits under both natural and controlled conditions presented in plants of this species.

Elevational sub_populations of *A. alpinum* in our study sites in Swiss Alps constitute a continuously conspecific band that spans an average of 1.4 km gradient from sheltered timberline to exposed alpine ridgetop. Despite the potential for stepwise gene movement between these closely adjacent sub_populations along these gradients , significant differentiation had been observed at isozyme loci in this study. Moreover , Nei's measures of genetic distance also showed that the sub_populations in higher elevations did give higher values on all three transects and a significant correlation had been found between genetic distance and differences of sub_population elevation ($R = 0.54$, $P = 0.02$).

In traditional view , the cline will be maintained by a balance between dispersal and selection (Felsenstein , 1976). Any gradient in these allele frequencies , due to history or to weak selection , will generate linkage disequilibrium in the cline , because two dissimilar populations are being mixed (Li and Nei , 1974). This disequilibrium , interacting with selection at the primary cline , will in turn produce a step in allele frequency , and gene flow will be reduced. Furthermore , the size of this step , at equilibrium , will be proportional to the gradient in allele frequency outside the region of interest (Barton , 1979). Altitude corresponds to environmental gradients. Rapidly changing environmental conditions along these gradients could result in asynchronous flowering , restricting gene flow among the sub_populations. Therefore , the population differentiation of *A. alpinum* observed along all three altitudinal transects in the study suggests that gene flow among the sub_populations may be too weak to overcome the effects of natural selection in favor of adaptations to local conditions , and that temperature variables may function as an at least major selective force in this case.

The investigation gave insight about geographical variation of *A. alpinum* populations at isozyme loci. Further reciprocal transplanting experiments and direct estimations of gene flow will conduct in the same localities in order to understand the adaptive significance of genetic differences found here.

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阿尔卑斯山黄花茅(*Anthoxanthum alpinum*) 沿海拔梯度的基因频率分布

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摘 要 在瑞士阿尔卑斯山的 2 个定点样地 ,黄花茅从森林线(海拔 1700 m)到山顶(海拔 2830 m)呈连续分布。在海拔梯度样带的最高和最低定样场所间的垂直距离差不多为 1000 m ,但 2 个定样场所间相距仅仅 1.4 km。在所研究的 3 个海拔梯度样带中 ,3 个同工酶位点 (*Px_1* , *Got_2* 和 *Mdh_1*)被观察到有统计意义的倾群变异。研究结果显示 :沿海拔梯度样带的亚居群间的基因流可能太弱不足以克服自然选择的影响 ,后者促使对局部环境的适应。在这种情况下 ,温度因子至少可能作为一种主要的自然选择力起作用。

关键词 阿尔卑斯山黄花茅 ,倾群变异 ,酶多态性 ,海拔梯度

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