Distribution of diploid sexual and triploid apomictic dandelions (*Taraxacum* sect. *Ruderalia*) along two altitudinal gradients in Switzerland

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Abstract

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The distribution of the cytotypes of *Taraxacum* section *Ruderalia* in relation to altitude was investigated along two altitudinal gradients, Chasseral (Jura) and Verbier (Alps). The populations were collected every 200 m in elevation and the flowering phenology was noted. Only diploid sexual plants were found at altitudes higher than 700 m. This is new for *Taraxacum* for which the diploid cytotype was considered infrequent, and even rare at high altitude. The distribution of the cytotypes is best explained by the survival of *Taraxacum* in nunataks of Jura and the Alps during glaciation, and the limited spread of the diploid during the subsequent warming. The triploid cytotype, with its better colonisation ability, would have largely colonised the previously glaciated areas, particularly in northern Europe.

Key words: Taraxacum, Asteraceae, sexual diploid, apomictic triploid, cytogeography, altitudinal distribution.

Introduction

The study of the detailed distribution of the cytotypes of sexual-asexual polyploid complexes is of prime importance to complete our general knowledge of polyploid complexes, and in particular to understand the respective colonising abilities of apomictic polyploids and sexual diploids and their relative fitness in diverse ecological conditions.

In Europe, *Taraxacum* section *Ruderalia* is composed of sexual diploid and apomictic triploid plants. The distribution of those two cytotypes has been surveyed throughout western, central and northern Europe (den Nijs & Sterk 1980, 1984, Elzinga et al. 1987, Roetman et al. 1988, den Nijs et al., 1990). Sexual diploids were found in two distinct areas. One corresponds to western Europe from the southwestern Netherlands and western Germany to the Pyrenées and perhaps further south. The second is located in central Europe from the Sudette

to Lake Balaton and from the eastern part of Austrian Alps to Romania. Between those and in northern Europe, only triploids have been found. This type of distribution of the diploid cytotype corresponds to a classic pattern deriving from the last glacial refuge from southern France and the Balkan region (Taberlet et al. 1998). The distribution of the diploid within its range is thought to be caused by both influences of climatic factors and vegetation history of these regions (den Nijs et al. 1990). According to den Nijs et al. (1990), the northern limit of the diploid should be due to climatic factors, following the fact that along this border it is restricted to warm and dry localities. The triploid cytotype is thought to have a wider ecological amplitude, allowing it to grow in a colder and wetter climate. In a more general way, polyploids are supposed to have a wider tolerance for diverse climates in particular for cold (Grime & Mowforth 1982, Bierzychudek, 1989).

The vast majority of the populations studied in *Taraxacum* are from low elevations. Although sexual plants have occasionally been found at very high elevation (up to 2390 m in the Swiss Alps) (den Nijs & Sterk 1980, 1984), their distribution along altitudinal gradients has not been analysed yet. The comparison of altitudinal and latitudinal distributions should allow to analyse the respective roles of ecological and historical factors.

According to the previous considerations, we hypothesised that the occurrence of the triploid cytotype would be positively correlated with altitude, thus mimicking the situation in the north. Such results would have favoured the ecological explanation of the distribution patterns with triploids having a wider tolerance for harsh climate.

Here, we describe the distribution of the cytotypes along two altitudinal gradients and their flowering phenology. Contrary to expectations, we found only diploids along those altitudinal gradients at the higher elevations.

Materials and methods

Populations were sampled in 200 m elevation intervals, from 550 to 1550 m at Chasseral (Neuchâtel) and from 1550 to 2350 m at Verbier (Valais), forming two altitudinal transects. In each one, plants were randomly collected in the pastures avoiding the edges, to determine their ploidy level (Table 1). In the two transects, the flowering phenology was noted every fourth day in counting the number of open capitulums per square metre, repeated in 10 randomly chosen places.

The ploidy level of the plants was determined either by chromosome counts or by flow cytometry (see Table 1). For the chromosome counts, root tips were pre-treated in 8 hydroxyquinoleine at 0.002 M for 2h15 and then fixed in Carnoy (ethanol/concentrated acetic acid; 3:1) for at least 24 hours. Tips were then transferred in cold acetic carmine for 2 hours, then gently heated to ~90 °C for 2–3 minutes and squashed on a microscopic slide in 45% acetic acid. In the case of flow cytometry, the ploidy level of the plants was determined with a facscan flow-cytometer (Becton Dickinson). For each specimen, a fresh leaf was placed in a petri dish and sliced using a razor blade in 0.5 ml of ice cold buffer. The buffer (pH 7.0) based on Galbraith et al. (1983) consisted of 45 mM $MgCl_2$, 20 mM 4-morpholine propane sulfonate, 1% Triton X-100 and 10 mM sodium metabisulfite. The stain, 20 µl iodium propidide, was then added. Finally, the homogenate was filtered through a 25µm mesh nylon screen. The mean fluorescence detected for a specimen is proportional to its DNA content per nucleus. The relationship between DNA content and ploidy level was determined by scanning diploid and triploid plants with known chromosome number (Table 1).

Results

The phenology was correlated with altitude. We found a delay of 5 to 14 days of the beginning of the blooming of *Taraxacum* for every 200 m in elevation (Fig. 1). For a given al-

Table 1. *Taraxacum* population samples from the two transects, Chasseral and Verbier. Collection date, number of analysed plants, method of analysis, ploidy level of the plants. Counts = chromosome counts, cyto = flow cytometry.

| Transect	Altitude	Collection time	Number of determined plants	Method of ploidy determination	2×	3×	4×
Chasseral							
Marnière de Hauterive	550	1996	100	counts	1	99	0
Villeret	750	1996	50	counts	50	0	0
Fauchette	950	1996 & 1999	50	cyto	49	0	1
Bugnenet	1150	1996 & 1999	50	cyto	50	0	0
Plan à l'Aigasse	1350	1996 & 1999	50	cyto	49	0	1
Petit Chasseral	1550	1996 & 1999	50	cyto	50	0	0
Total			*350*		*249*	*99*	*2*
Verbier							
Les Creux	1550	1996	50	counts	50	0	0
Le Sonalon	1750	1996	25	counts	25	0	0
Bisse de Levron	1950	1996	25	counts	24	1	0
Grand Plans	2150	1996	25	counts	25	0	0
Savoleyre	2350	1996	25	counts	24	1	0
Total			*150*		*148*	*2*	*0*
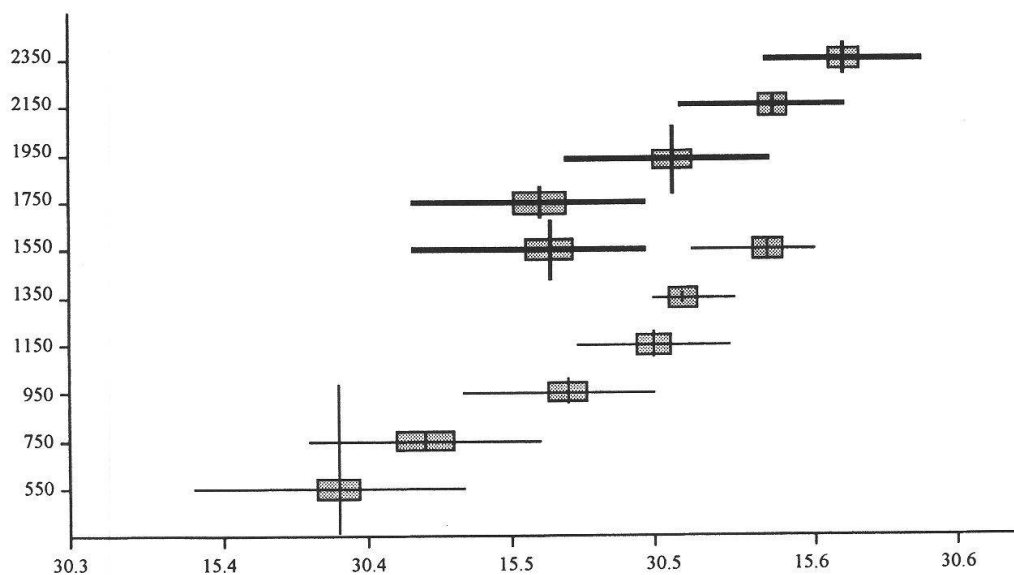
Fig. 1. Phenology of the flowering of *Taraxacum* along the two transects according to date and to altitude; thin line – Chasseral, bold lines – Verbier: period of flowering (horizontal bar), density at the peak of flowering (vertical bar, the bold vertical bar on the right represents a density of 50 capitulums per square meter) and standard deviation (box).

titude on a transect, the blooming period lasted from 10 to 25 days. The peak densities were approximately in the middle of the blooming period, with typically 25 to 50 capitulums per square metre. The Hauterive population had up to 160 capitulums per square metre at peak blooming. The determination of ploidy levels along the two altitudinal transects revealed the almost exclusive presence of diploids above 700 m elevation (Table 1).

In the Chasseral transect, the lowest population (550 m) was triploid at 99%, while all the higher populations were diploid at the exception of two tetraploid plants. In Verbier, all the populations (from 1550 m to 2350 m) were diploid at more than 98%.

Discussion

In the Alps the vegetation period is reduced by 7 days per each increase of 100 m in elevation (Gensler 1946), which corresponds roughly to a delay of 3.5 days of the beginning of the growing season, and a shortening of 3.5 days at its end. The delay of 5 to 12 days that we observed at the beginning of the blooming period of *Taraxacum* every 200 m elevation (i.e. 2.5 to 6 days per 100 m) corresponds to the values found by Gensler (1946). This delay prevents effective pollen transfer between localities separated by more than 400 m in elevation. Hence, it slows down the gene flow by pollen along altitudinal gradients, considering that a pollinator (honeybee for example) has normally a greater range of action. Gene flow may nevertheless occur stepwise, considering several generations.

The flowering period was earlier in Verbier than in Chasseral for similar elevations. This is certainly due to slope orientation, Verbier is facing south and Chasseral north. The length of the flowering period was only slightly influenced by the altitude, with a reduction of less than 2 days per 100 m elevation in Chasseral and only 1 day for the same elevation interval in Verbier. *Taraxacum* flowers very early in the season, only a few weeks after the snow has melted, and has then enough time to achieve seed production during the season, even at high altitudes.

The density of simultaneously blooming capitulums at the peak of the flowering was probably an underestimate of the density of individuals in the fields, as only a portion of them flowered. There was a very strong density of *Taraxacum* in the pastures. One of them (Hauterive) was literally covered with dandelions, 160 capitulums per square metre being an average value, some places having more than 300 capitulums per square metre. On a dry limestone pasture, one population had even finished flowering within 10 days, which was particularly short since flowering time could last up to 30 days.

In the previous studies of the distribution of the cytotypes of *Taraxacum* section *Ruderalia*, western, central and northern Europe were investigated (den Nijs & Sterk 1980, 1984, Elzinga et al. 1987, Roetman et al. 1988, den Nijs et al. 1990). Although the geographical distribution of the cytotypes over these areas is well known, their altitudinal distribution has not been investigated.

The exclusive presence of diploids above 700 m elevation was not expected, although it confirmed the detailed distribution study in the Neuchâtel region of Meirmans et al. (1999). These results contrast with the analysis of plants collected in Verbier by van Soest, which ploidy level was determined by den Nijs & Sterk (1984), and showed roughly 50% of triploids. That discrepancy is probably explained by the fact that van Soest collected the plants along the roadsides (den Nijs *pers. com.*), whereas we collected them in the middle of homogenous pastures. The particular conditions occurring at roadsides could have favoured presence of triploids.

Polyploids and in particular apomictics are usually believed to be more adapted to harsh climate (high altitude and northern areas) and are consequently more common in these are-

as (Grime & Mowforth 1982, Bierzychudek 1989). In the case of *Taraxacum*, the latitudinal trend is clear: only triploids colonise the far north, while diploids are restricted to warm dry microclimates along their northern margins (den Nijs et al. 1990). At high altitudes, our results demonstrate the almost exclusive presence of sexual diploids. However, they are limited to two transects (one in the Jura the other in the Alps), a wider sampling across the alpine range would be necessary to confirm their importance.

These results are in accordance with the analysis of Favarger (1957, 1967, 1985) on the percentage of polyploids in the Alps, in southern Greenland and in Spitzbergen. According to his observations, the proportion of polyploids is much lower at high altitudes in the Alps, than in the north. It is hypothesised that during the last glacial period, the flora survived only on the high altitude unglaciated refuges (nunataks). After glaciations, diploids colonised the ice-free areas with less efficiency than polyploids, but remained on nunataks and their surroundings (Favarger 1975). This hypothesis is reinforced by the facts that polyploid *Taraxacum* are apomictic, hence having a better colonising efficiency than sexuals. Diplosporic apomixis may increase colonising ability by the fact that no pollen source is needed to create a new settlement. Therefore, a single plant is able to form a new population.

The present distribution of the cytotypes, if it is confirmed to be a general pattern in the Alps and in Jura, is probably best explained with historical factors. The western and central Europe "diploid areas" are located on or very close to glacial refuges of the last glaciation period (Taberlet 1998). In addition, Chasseral (Jura) was partly free of ice at this time, while Verbier (Alps) is at the vicinity of a nunatak region (Stehlik 2000). If ecology was the main determinant of the present distribution, the altitudinal distribution of the cytotypes would be similar to the latitudinal one, with triploids present in the harsher climates of high altitude.

While historical factors should be the main determinants of the general patterns of the cytotypes, ecological differentiation occurs at a local scale. Ecology is probably responsible for most of the local particularities of distributions within the zones where both cytotypes occur, and in particular at the northern border of the range of diploids (den Nijs et al. 1990). In the area of Neuchâtel at low altitude, local ecological differentiation was found, with triploids being favoured by disturbed habitats and diploids restricted to relatively undisturbed fields. At higher altitude there were mainly diploids, and the few triploids were limited to highly disturbed places (Meirmans et al. 1999). Local ecological differentiation has been also observed repeatedly in other polyploid complexes (Lumaret 1988, Jay et al. 1991, Felber-Girard et al. 1996).

Résumé

La distribution des cytotypes de *Taraxacum* section *Ruderalia* en relation avec l'altitude a été analysée le long de deux transects altitudinaux, Chasseral (Jura) et Verbier (Alpes). Les populations on été récoltées à des intervalles de 200 m d'altitude et la phénologie de la floraison a été notée. Au-dessus de 700 m, seul le cytotype diploïde sexué a été trouvé. Cette répartition est originale pour *Taraxacum,* dont le diploïde était supposé être peu fréquent, voire même rare aux altitudes élevées. La distribution actuelle des cytotypes s'explique le mieux par la survie des pissenlits au sud de l'Europe et sur les nunataks durant la dernière

glaciation, puis par la recolonisation limitée du diploïde durant le réchauffement qui a suivi. Le cytotype triploïde, avec sa meilleure capacité de colonisation, aurait colonisé les zones précédemment glaciées, en particulier au nord de l'Europe.

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