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# SENSITIVITY OF THE FOUR CYTODEMES OF *ANTHOXANTHUM ODORATUM* L. S. LAT. (POACEAE) TO *PUCCINIA SARDONENSIS* GÄUMANN (UREDINALES)

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*Summary*

Attempts to infect the four cytodemes of *Anthoxanthum odoratum* L. s. lat. (Poaceae) with *Puccinia sardonensis* Gäumann (Uredinales) were successful with half the individuals of *A. alpinum* A. & D. Löve (diploid and tetraploid) but not with those of *A. odoratum* s. str. (diploid and tetraploid). For each cytodeme, the sensitivity to the parasite was not dependent on the origin of the material and no correlation was established between the distribution of the rust and that of susceptible individuals. Susceptibility and resistance to *P. sardonensis* would therefore probably be long-established characteristics which originated at the time of differentiation of the two diploid taxa of *A. odoratum* s. str. and of *A. alpinum* but which preceded their respective polyploidization phases. Resistance to infection would have no adaptive value since resistant *A. odoratum* is not exposed to infection in nature and probably never has been. These results support the division of *A. odoratum* s. lat. into *A. alpinum* and *A. odoratum*.

*Résumé*

Des essais d'infection des quatre cytodèmes d'*Anthoxanthum odoratum* L. s. lat. (Poaceae) par *Puccinia sardonensis* Gäumann (Urédinée) réussissent sur la moitié des individus d'*A. alpinum* A. & D. Löve (diploïde et tétraploïde) mais jamais sur ceux d'*A. odoratum* s. str. (diploïde et tétraploïde). Pour chaque cytodème, la sensibilité au parasite est indépendante de l'origine du matériel et aucune corrélation n'a été établie entre la distribution de la rouille et celle des individus sensibles. La susceptibilité et la résistance à *P. sardonensis* représenteraient donc des caractères anciens dont l'apparition serait contemporaine de la différenciation des deux taxons diploïdes d'*A. odoratum* s. str. et d'*A. alpinum* mais antérieure à leurs phases respectives de polyploïdisation. La résistance à l'infection n'aurait pas de valeur adaptative puisque *A. odoratum* résistant n'est pas exposé à l'infection dans la nature et ne l'a vraisemblablement jamais été. Ces résultats témoignent de l'indépendance taxonomique d'*A. alpinum* et d'*A. odoratum*.

## *Introduction*

Reactions to a pathogenic agent may reveal genetic differentiation among collective species and, in favorable cases, facilitate the understanding of phylogenetic relations between infraspecific taxa. The case of the polyploid complex *Anthoxanthum odoratum* L. s. lat. (Poaceae) is significant in this respect. Gaümann (1945) described a new species of Uredinales, *Puccinia sardonensis,* a rust with a heteroiecious cycle involving two hosts: *Callianthemum coriandrifolium* Reichenb. (Ranunculaceae) for the formation of aecidiospores and *A. odoratum* s. lat. for the formation of uredo- and teleutospores. Gaümann succeeded in infecting alpine ecotypes of *Anthoxanthum* but never those from the plains. Gaümann, who found no morphological differences between the alpine and plain populations, concluded that they represent distinct biological races.

On the basis of his cytological observations, Favarger (1956, 1963) assumed that plants susceptible to *P. sardonensis* belong to the diploid cytodeme *A. alpinum* ($2n = 10$), described

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Table 1. Sensitivity of the four cytodemes of *Anthoxanthum odoratum* L. s. lat. to *Puccinia sardonensis* (+: infected plant, –: healthy plant).

| Cytodeme or reference number | Origin | Result | Proportion of plants infected by cytodeme (%) |
|---|---|---|---|
| *A. alpinum* 2X (same origin as *Puccinia sardonensis*) | | | |
| 84-1425-1 | Switzerland, Saint-Gall, Pizolhütte, 2250 m (KF).[a] | + | 55 |
| -2 | ibid. | + | |
| -3 | ibid. | – | |
| -4 | ibid. | + | |
| -5 | ibid. | + | |
| -6 | ibid. | – | |
| -7 | ibid. | + | |
| -8 | ibid. | – | |
| -9 | ibid. | – | |
| -10 | ibid. | – | |
| -11 | ibid. | + | |
| *A. alpinum* 2X (other origins) | | | |
| 83-1209-32 | Germany, Bade-Wurtemberg, Feldberg, 1440 m (FP). | – | 57 |
| 83-1397-1 | France, Alpes-Maritimes, Col des Champs, 2100 m (JV). | + | |
| 83-1214-3 | France, Vosges, Hohneck, 1300 m (FP). | – | |
| 82-1735-2 | Switzerland, Grisons, Julierpass, 2280 m (FR). | + | |
| 83-1274-2 | Switzerland, Vaud, Aiguilles de Baulmes, 1540 m (F). | + | |
| 82-1583-26 | Switzerland, Vaud, Chasseron, 1500 m (F). | + | |
| 83-1303-2 | Switzerland, Vaud, Suchet, 1510 m (FK). | – | |
| *A. alpinum* 4X | | | |
| 82-1615-3 | France, Ain, la Maréchaude, 1510 m (FK). | – | 50 |
| 82-1616-1 | France, Ain, Reculet, 1470 m (FK). | – | |
| 83-1171-2 | France, Cantal, Puy de Bataillouze, 1680 m (FG). | + | |
| 82-1534-31 | France, Cantal, Puy Mary, 1580 m (F). | + | |
| 83-1184-3 | France, Isère, Charmant Som, 1750 m (FG). | – | |
| 82-1535-12 | France, Puy-de-Dôme, Croix-Morand, 1400 m (F). | – | |
| 82-1538-17 | France, Puy-de-Dôme, Supeyres, 1330 m (F). | + | |
| 82-1645-2 | Switzerland, Valais, Bec-du-Corbeau, 1990 m (F). | + | |
| 82-1920-4 | Switzerland, Vaud, Dôle, 1660 m (FK). | + | |
| 83-1301-2 | Switzerland, Vaud, Mont Tendre, 1670 m (FK). | – | |
| *A. odoratum* 2X | | | |
| 83-251-12 | Greece, Crete, Aghia Irini, 600 m (KM). | – | 0 |
| 83-249-5 | Greece, Crete, Nida, 1400 m (KM). | – | |
| 83-250-1 | Greece, Crete, Volikas, 1500 m (KM). | – | |
| 83-1007-10 | Yugoslavia, Istra, Pican, 270 m (FP). | – | |
| 83-1007-12 | ibid. | – | |
| 82-1440-1 | Yugoslavia, Istra, Porec, 110 m (FP). | – | |
| 82-1440-2 | ibid. | – | |
| 82-1442-1 | Yugoslavia, Slovenia, Grgar, 290 m (FP). | – | |
| 83-1047-27 | Yugoslavia, Slovenia, Komen, 320 m (FP). | – | |
| 83-1047-28 | ibid. | – | |
| *A. odoratum* 4X | | | |
| 83-1172-2 | France, Cantal, Puy de Bataillouze, 1300 m (FG). | – | 0 |
| 83-1212-1 | France, Haut-Rhin, Tête des Faux, 1130 m (FP). | – | |

Table 1. Continued.

| Cytodeme or reference number | Origin | Result | Proportion of plants infected by cytodeme (%) |
|---|---|---|---|
| 83-1185-3 | France, Savoie, Mont Revard, 1480 m (FG). | – | |
| 82-1445-8 | Italy, Friuli, Pezzeit, 610 m (FP). | – | |
| 82-1731-3 | Switzerland, Grisons, Jenins, 1020 m (FR). | – | |
| 82-1740-4 | Switzerland, Grisons, Scuol, 1550 m (FK). | – | |
| 82-1812-1 | Switzerland, Soleure, Hasenmatt, 1420 m (FK). | – | |
| 82-1614-2 | Switzerland, Vaud, Ferreyres, 625 m (F). | – | |
| 82-1439-13 | Yugoslavia, Slovenia, Golac, 605 m (FP). | – | |

[a] Collectors (F = F. Felber; FG = F. Felber, C. and S. Giroud; FK = F. Felber and Ph. Küpfer; FP = F. Felber and J. Pfister; FR = F. Felber and M. Krähenbühl; JV = Ph. Jacot and C. Vuille; KF = Ph. Küpfer and E. Fortis; KM = Ph. Küpfer and B. de Montmollin).

by Löve and Löve (1948), and that the resistant plants correspond to the tetraploid taxon *A. odoratum* (2n = 20). This hypothesis was quoted by Gäumann (1959). Löve (1960) saw in Gaüman's results an additional argument in favor of separating *A. alpinum* from *A. odoratum* s. lat. Nevertheless, these authors thought that the difference in sensitivity between diploid *A. alpinum* and tetraploid *A. odoratum* was the effect of polyploidization. Hedberg (1967), however, thought that without chromosome counts of plants exposed to infection no conclusions could be drawn.

Analysis of the karyotypes allowed Teppner (1970) to recognize not two but four cytodemes for *A. odoratum* s. lat.: diploid (2n = 10) and tetraploid (2n = 20) *A. odoratum* s. str. and diploid (2n = 10) and tetraploid (2n = 20) *A. alpinum*.

Whereas the autoploidal origin of tetraploid *A. alpinum* is not in dispute (Hedberg, 1970; Teppner, 1970), that of tetraploid *A. odoratum* is still under discussion. Böcher (1961), Borril (1963), Jones (1964) and Teppner (1970) believe that *A. odoratum* is an allotetraploid derived from a cross between *A. alpinum* and another diploid taxon. However, Hedberg (1970) suggests that *A. odoratum* could be an autotetraploid of diploid *A. alpinum* where chromosomes could have undergone structural changes.

In Europe, *A. odoratum* s. str. is essentially a species of the plains, the diploid cytodeme extending to central Mediterranean areas and the Balkans. The tetraploid taxon, favored by human activity, is widespread at low and medium altitudes. Diploid *A. alpinum* grows in northern Scandinavia and in the greater part of the central European and Italo-Balkanic mountainous regions. It is replaced, always at high altitudes, on south of the Jura mountains, on the northwestern fringe of the Alps and in the Massif Central, by the tetraploid cytodeme (Hedberg, 1970; Teppner, 1970; Felber, 1986 and unpublished).

The second host, *Callianthemum coriandrifolium* has a narrower distribution. It is a plant of the alpine zone in the Alps and the Carpathians.

The presence of the parasite *Puccinia sardonensis* is reported in the occidental and central Alps as well as in the Tatras (Gaümann, 1959).

This paper repeats Gäumann's experiments (1945) but on karyologically controlled material. The reaction to infection by the rust is established for each cytodeme and the geographical distribution of parasite sensitivity is determined.

## *Material and Methods*

Several individuals of *C. coriandrifolium* covered with *P. sardonensis* aecidia were collected by Ph. Küpfer and E. Fortis west of the Pizolhütte (Saint-Gall, Switzerland). Eleven

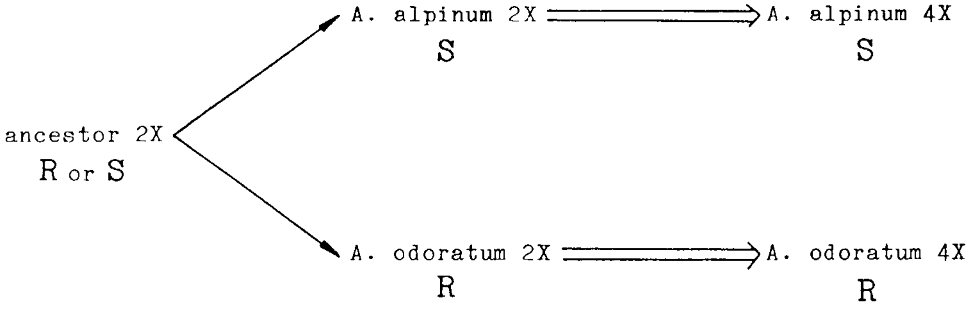

*Fig. 1.* Phylogenesis attempt on *A. odoratum* s. lat. in relation with the sensitivity to *P. sardonensis.* → = gradual speciation, ⇒ = autopolyploidy, R = resistant, S = susceptible.

plants of diploid *A. alpinum* were collected in the same locality. In addition, ten individuals of each cytodeme from various natural origins were used in this study (Table 1).

A priori, the optimal conditions for infection of *Anthoxanthum* by *P. sardonensis* were unknown to us. Therefore, plants of *Anthoxanthum* and of *Callianthemum* were placed in alternate rows under glass cloches or under a frame covered with plastic. The two systems assure high humidity, that of the frame, however, being slightly lower than that of the glass cloches. Infection was favored by rubbing the *Anthoxanthum* leaves with mature aecidia. The plants were observed regularly and, after two months, the uredospores and teleutospores of the rusts were determined by light microscope on the basis of the criteria laid down by Gaümann (1959).

## *Results and Discussion*

For each cytodeme, the proportion of plants susceptible to *P. sardonensis* was the same, regardless of the material used for the experiment (glass cloches or frame). We have thus grouped the results in Table 1.

After two-month exposure to infection, half of the *A. alpinum* (diploid and tetraploid) individuals showed uredospores and sometimes teleutospores on the leaves. The plants of the two cytodemes of *A. alpinum* from various localities and those of the station from which *P. sardonensis* originates were infected in the same proportion. On the other hand, none of the *A. odoratum* individuals (diploid or tetraploid) developed the fungus.

The cycle of *Puccinia sardonensis* has been described only for the alpine habitat so that culture under cover at 480 m probably does not represent optimal conditions either for the hosts or the parasite. The plants of *A. alpinum* which remained healthy more likely present a chance reaction to the experimental conditions rather than genetic resistance. However, the resistance of certain individuals of *A. alpinum* to the fungus cannot be excluded.

Other species of Uredinales, *P. coronata* Cda. or *P. graminis* Pers., for example, attack all four cytodemes of *A. odoratum* s. lat. The resistance of *A. odoratum* s. str. to *P. sardonensis* is thus very specific.

In the Alps, *Anthoxanthum* plants susceptible to parasite infection are high-altitude plants (Gäumann, 1945) corresponding, as Favarger (1956, 1963) supposed, to *A. alpinum.* However, *A. alpinum*'s sensitivity is not limited to the diploid race, a geographical region, or the distributions of *C. coriandrifolium* and *P. sardonensis.* It was possible to infect diploid and tetraploid plants of *A. alpinum* from the Jura mountains and from the Massif Central, although the aecial host and thus the rust are absent from these regions. Likewise, resistance to the parasite is uniform throughout the range of the two cytodemes of *A. odoratum.*

Resistance to infection would have no adaptive value since resistant *A. odoratum* is not exposed to infection in nature and probably never has been. It would be interesting, furthermore, to infect Scandinavian plants of *A. alpinum* and Japanese individuals of *A. nipponicum* Honda. This last species (2n = 10) is thought to be identical with *A. alpinum* (Tateoka, 1966; Hedberg, 1967; Löve and Löve, 1968).

### *Conclusions*

Our results reflect a close relationship between the two cytodemes of *A. alpinum* on one side and of *A. odoratum* on the other. Although autopolyploidy of *A. alpinum* is known, that of the diploid *A. odoratum* has never been proposed. This hypothesis seems probable to us (Fig. 1), but needs other approaches to verify it (Felber, research in progress).

Sensitivity to *P. sardonensis* is independent of the ploidy level. The observed differences would thus be contemporary with the differentiation of the two species, but would precede their respective polyploidization phases. We do not know, however, if their common ancestor was susceptible or resistant.

This paper brings a further argument in favor of splitting *A. odoratum* s. lat. into two species, but does not justify it in itself. We do not know the genetic determinism of the resistance, whereas the number of the genes involved in this phenomenon clearly influences the taxonomic value.

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