Ecological setting and requirements of *Pinguicula vulgaris* L. in the Champagne state of France, close to paris

L. EGENDRE and T. CIESLAK • University of Reims Champagne-Ardenne • Laboratory of Plant Biology and Physiology • UFR Sciences • B.P. 1039 • 51687 Reims Cedex 2 • France •
Email: laurent_legendre@hotmail.com
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INTRODUCTION

The genus *Pinguicula* which accounts for about 10% of all carnivorous plants drives an increasing interest from the hobbyist as well as from the professional scientist. However, emphasis has mostly been placed on their carnivorous character or their horticultural potential and beside some scarce and recent publications, virtually no information is available on their ecological needs as a green plant. In this report, we bring the first description of the ecological setting in which three populations of *P. vulgaris* thrive close to the city of Reims (Champagne state - France). After a quick comparison with other *P. vulgaris* populations, we'll try to raise some hypothesis on the ecological requirements of this species and on its protection mangement.

OBSERVATIONS

1- Distribution of *P. vulgaris*

P. vulgaris has one of the largest distribution area of all *Pinguicula* species. It covers most of the northern part of Northern America, Greenland, Iceland and a large part of Europe all the way to the Oural mountains and the Mediterranean sea (Fig. 1).

This large geographical distribution is in total contrast with most other *Pinguicula* species which can only be found on small isolated locations. Only *P. macroceras*, *P. alpina* and *P. villosa* also have a relatively large distribution area. *P. macroceras* is, however, a close relative of *P. vulgaris*, and *P. alpina* and *P. villosa* only thrive under one given ecological conditions in contrast to *P. vulgaris* which can be found at low or high altitude as much as high north close to the glaciers edge or in countries bordering the Mediterranean sea.

A close look at the distribution of *P. vulgaris* in France reveals that this species thrives in several discrete areas (Fig. 2). It is found on all mountain chains (Alps, Pyrenees, central massif, Jura and Vosges) at altitudes which are generally greater than 1000 m except for some rare populations which have been described at the bottom of the Vosges mountains in Alsace and in Jura. Interestingly, *P. vulgaris* can also be found on relatively flat lands at about sea level in a large area centered around Paris. There is, however, no mention of this species on a large oceanic strip on the western, northern and southern side of the country and in the valleys that separate the various mountain chains.

Figure 2 also shows that low-land sites are submitted to the highest environmental pressure and are vanishing as we speak. The countryside around the city of Reims (Champagne state - 150 km east from Paris) is thus very lucky to host some of the last remaining plants still growing under such conditions. These last survivors are very rare and grouped in discrete sets that are isolated from each other by large fields and cities. No precise map is shown to help protect them from human greed.

2- Description of the sites under study

The 3 sites under study are more or less located on a 20 km long east-west line where the city of Reims stands in the middle. The western site, close to the city of Neuf Ans is by far the largest one. It hosts more than 1000 individuals on a 1 km long, 10 m wide, seepage area located on a south-facing slight slope. This large population is in fact split into 3 unequal sets of plants. A small one (about 20 individuals) is found on a drainage ditch just before the seepage forms an alkaline bog. Another one (containing about 100 plants) develops in a forest opening recently made by big engines while removing an electrical line. At this site, most plants are found on the sides of the large holes made by the trucks wheels. Finally, the largest plant set is found in a horse field in between the two other populations. Noteworthy, most of the *Pinguicula* in the horse field are found on the north-facing sides of the small dirt mounds (20 to 30 cm high and wide) made by the horses as they peddle through the wettest areas of their field.

About 5 km away from Neuf Ans, a small population of about 20 individuals thrives in an alkaline bog close to the city of Chenay. As for most alkaline bogs, this one is not totally flat and faces westward. It is invaded by a local bog grass and most *Pinguicula* are found along a natural trail made by wild deers. Leaf rosettes stand at the water edge.

The last *Pinguicula* site lies on a small hill lock close to the city of Berru. Two groups of plants of about 50 and 20 individuals respectively thrive close to each other on its western slope on a small seepage area located on a forest trail just above an alkaline bog. This trail is largely used by horses and motorcycles.

Even though apparently very dissimilar, these 3 sites share some obvious common features (summarized on Fig. 3):

- all are located in very open areas, on trails used by large animals or motor engines and on small slopes exactly where water starts flowing out of the earth to form a small seepage. This water may not be seen during dry periods but the earth at this point always feels wet to the touch. Alkaline bogs are found at or just below the plants.
- all are found just below a forest area (no field above) where acid-loving trees such as chestnut, oak and birch trees can be found. These slightly acidic areas are rare in a state mostly covered by chalk. They are often fairly sandy too.
- All *Pinguicula* sites contain a high level of clay. This water-impermeable soil layer is what forces infiltrated water to flow outside to generate the seepage described above.

3- Importance of the sites under study

One concern about drawing any conclusion from the study of only 3 sites in an agriculturally highly developed area is that these sites may just be the only places where no field has swapped away a natural population. And it is true that farmers never develop wheat fields on sandy soils where springs are present. But information gathered from local botanists or ancient flora indicates that the sites under study are representative of all of the places where *Pinguicula* used to live in the Champagne State. Moreover, they are among the last known remaining sites (at least the last ones we know of). We found no document indicating how abundant these plants used to be in the past. But, the history of cultivation practices (only sheep breeding on large bogs followed recently by pine farming and even more recently by wheat, grapes, beets...) and ancient floral records suggest that they must have been very common up to 100-20 years ago.

4- Physiological and morphological characteristics

All of the 3 populations which have been studied in the Champagne state share absolutely identical physiological and morphological characteristics except for their flower color which is slightly more pink westward and more blue eastward. They can easily be identified as *P. vulgaris*. However, because *P. vulgaris* is a highly variable species and because these plants have been isolated for quite some time, they differ slightly from the type specimen.

As for all known *P. vulgaris*, the plants present in the Champagne state form small rosettes of oblong to slightly lanceolate leaves out of which flowers come singly (Fig. 4). The short petal lobes do not overlap and the corolla never opens fully (Fig. 5). It is blue to purple with a large white dot at the bottom of the throat entrance which is covered by many hairs. A single dark purple line runs through the center of the white dot of the largest flowers. The petals fuse into a spur which is slightly bent, has about the same size as the lobes and is thin but not pointed.

Still, after having observed *P. vulgaris* specimens from several locations during cultivation experiments (great lake region of North America, Iceland, Slovenia, Vosges, Jura, Alps) and sometimes in their natural habitat, I came to the conclusion that the plants growing in the Champagne state display some minor, but distinct, morphological features. The first striking feature is their small size. The rosettes are small and nearly never exceed 7 cm in diameter. Most blooming plants only measure 3 to 5 centimeters across. The flower stalks are about half as thick as normal. The calyx is also smaller than normal with more rounded sepals while the corolla does not seem to be any smaller than usually observed. Local plants never produce more than 2 flowers per season while most other *P. vulgaris* can easily generate at least 5 flowers and sometimes up to 10 under optimum growing conditions. The winter-resting buds display a normal size and shape with their outer scales covering the entire bud. They do not bury themselves under the ground. They, however, generate very large quantities of daughter buds (20 to 50 per mother bud) in contrast to all of the other *P. vulgaris* we are growing and which only produce a maximum of 2 daughter buds each year and most often none. Another interesting distinguishing feature is found in the seed cap which is perfectly round. This seed cap shape has rarely been seen (in one Norway island population for example - J. Steiger personal communication) and differs from the typical pointed pear-shaped seed cap of other *P. vulgaris*. All of the above morphological characteristics are kept under cultivation (5 years of observation). However, a comparison with a larger number of *P. vulgaris* specimens will be required to appreciate the importance of the observed differences.

But the most distinct feature of the plants growing in the Champagne area lies in their growing cycle. This has been best seen when *P. vulgaris* plants originating from different places (see list of studied populations above) have been grown in the same pot at the city of Reims. Local plants indeed break dormancy at least 3 weeks after the others and generate their first leaves when others need to be pollinated. Then, they will survive the hot summer months without returning to dormancy which other *P. vulgaris* do by the end of August. On the contrary, they will keep on producing new leaves all the way through the end of October. Leaf production is indeed important in the fall and it is thus of no surprise to see that a seed which has been planted in the spring will bloom two springs later and sometimes even the next one. Other *P. vulgaris* will require at least an extra year. These growing characteristics have been seen repeatedly 5 years in a raw.

All of the *Pinguicula* living close to Reims produce very large amounts of seeds (about 50 per seed cap) out of which more than 95% will germinate the next year. Two years in a row, I've tried to pollinate *P. mundii* with *P. vulgaris* coming either from Iceland or from Reims (2 times 5 crosses each year). The first cross always gave more than 80 seeds per capsule while the other one never gave more than 5 seeds. However, all of the seeds that have been collected have germinated just fine.

Because of the small size and round nature of *P. vulgaris* chromosomes, all of our attempts to evaluate the chromosome count of the Reims plants have failed. Between 26 to 30 chromosomes have been counted but we know this is an underestimated value. We do not know how far we are from the correct number but we doubt it will go up to the expected 2n=64 which has been described for other *P. vulgaris*. Clearly, more work is needed in this area because a smaller chromosome count could explain the stunt nature of these plants.

5- Seed and pollen shape

Electron microscope pictures of Reims *P. vulgaris* seeds and pollen are respectively shown in Figure 6 and 7 for future reference in later comparative studies. As for other *P. vulguris*, the seeds of the local plants exhibit an ovoid shape and are larger and not as elongated as for other *Pinguicula* such as *P. mundii* fir example. Pollen grains are round and shaped like pumpkins.

6- Throat hair structure

As previously noted by Casper (1966), the structure of the hairs at the entrance of the flower throat have some taxonomic value. In the case of the Reims plants, most are made of 3 elongated cells which length and pigmentation reduces by half as we go up (Fig. 8). They then bear 6 to 10 white round cells which pile up on top of each other like beads on a string. Occasionally, one of these round cells has a daughter one at its own level.

7- Influence of light on plant development

In all sites, it is clear that the healthiest individuals are found in very open areas with no direct sunlight. The presence of heavy shade under tall weeds or trees produces etiolated plants and is apparently lethal. Similarly, on bare soils and under direst sun light the rosettes are small and slightly pigment themselves in red.

8- Influence of water and wind on plant development

The *Pinguicula* growing close to Reims do not seem to be dependant on the quantity of water that is available to their roots. They do just as well in Chenay with their rosettes at the water edge as in the two other sites which are rarely damp (only in the spring and late in the fall) and are most of the time just moist. Most parts of the site close to Neuf Ans even dry out on surface (only moist 1 cm below the ground surface) during the hot month of august.

To the contrary, local *Pinguicula* are really sensitive to air humidity. They do poorly in windy places and really thrive best in restricted areas with little if not no air movement and with a saturating air humidity.

9- Influence of air temperature on plant development

All 3 sites are exposed to the same temperatures (Tab. 1). These can be really cold in the winter (uner -15°C) and hot in the summer (over 30°C). More importantly, the Champagne state is subjected to a continental weather with rapid and unpredictable temperature changes. Relatively warm winter days thus occur every year (over 10°C in December-January). These fool many garden plants such as *Prunus* sp. trees which may bloom on January to see their flowers freeze later on. Late frost also occur most years all the way to April (-5.5°C on April 21, 1997). Similarly, warm days are seen all the way to October (over 20°C).

10- Prey capture

Prey capture seems to be more abundant at night or early morning. More insects are also trapped in the spring. The main captured preys are small flying insects that resembles a fruit flies.

11- Geological setting

A geological study of all 3 sites where *Pinguicula* live indicates that the plants are always located on mixed-soil areas (mixed over geological ages) containing chalk, clay and sand (Precise geological maps have been drawn by the authors and are available in the French language upon request to the authors). This information is that much more relevant that the sites under study exhibit no top soil layer and picking up a handful of soil mix allows one to observe some chalk grains (1-2 mm wide) and silica particles (0.1 mm diameter) embedded in clay. Significant quantities of dead leaves originating from the nearby forests are also present. Their presence is normally very rare in most parts of the state where the very basic pH's of the soil induce their rapid decomposition. These plant debris are responsible for a small acidification of the top soil layer of the *Pinguicula* sites which display measured pH values of only 6.5 (even with the presence of chalk).

12- Cultivation experiments

Local *Pinguicula* always end up dying in a mix of acidic peat moss and sand. Most deaths do not occur during the vegetative period but rather in early spring when winter buds break dormancy. At this stage, they seem to die under the attack of a phytopathogenic fungus *Pythium* sp.. The addition of chalk allows survival. Optimal growth will be obtained when a small quantity of leaf mold is also added to the potting mix.

Discussion

1- *P. vulgaris* is a very adaptive and variable species

For anyone who is used to observe *Pinguicula* on top of mountains or very high north, it is somewhat surprising to learn that *P. vulgaris* naturally thrives 100 m above sea level and 150 km east from Paris, on one of the flattest place in Europe where summer temperatures easily go above 30°C. But this is to forget that *P. vulgaris* has an unusually large distribution area and is able to develop under several ecological conditions. Its high adaptability has been hypothesized to derive from its high ploidy level (Steiger, 1998) which in turn may be an indication that this species is one of the most modern of all european *Pinguicula* (Steiger, 1998).

High adaptability and survival in isolated and distinct ecological environments has opened the path to microevolutionary changes as exemplified by the individuals living in the Champagne state. These *Pinguicula* used to be part, only 40 years ago, of a very large colony that was thriving around Paris. This colony is, however, totally isolated from other *P. vulgaris* (the closest relatives are in the Vosges 350 km away) and has probably been so since the end of the last glacial age some 8,000 years back. However, morphological differences are not solid enough (such as size differences) or so unique to these individuals (round capsule for example) to justify their taxonomic separation from or within the *P. vulgaris* complex as a new variety or subspecies. For further information on *P. vulgaris* subspecies or varieties please refer to Casper (1966).

2- The Reims *P. vulgaris* are adapted to local climatic conditions

The distinct growing cycle of the Champagne state *P. vulgaris* can be seen in the light of a close adaptation to local growing conditions. Unlike other *P. vulgaris*, local plants indeed do not break dormancy as soon as the weather warms up in the spring and wait until the last frost is over. They are thus insensitive to the many alternating periods of frost and warmth seen between February and April. Additionally, local plants are the only *P. vulgaris* we are growing that do not go into dormancy during the hot days of august and that are insensitive to a partial drying of their soil. This will allow them to take advantage of the traditionally nice days of the fall (Tab. 1) to develop many new leaves and accumulate energy for the winter. This is even a perfect moment to accumulate energy since no flower are to be formed at this time.

3- Benefits and cost of carnivory

An accepted advantage of carnivory is that it allows plants to feed on animals to compensate for poor soils. Well, this is a very debatable point when *Pinguicula* are concerned (reviewed in Juniper *et al.*, 1989; Legendre, 2000). A scientific study has indeed suggested that these plants will beneficiate more from a good soil than from preys (Aldenius *et al.*, 1983). Our cultivation experiments also show that adding some nutrient-rich leaf mold to their growing medium will result in enhanced growth. This statement has, however, been tempered since by two studies which demonstrate that the soils on which *Pinguicula* normally grow on must be poor enough to allow animal feeding to speed up growth and development of seedlings and adult plants (Thoren and Karlsson, 1998; Worley and Harer, 1999).

However, a hidden and never stated cost of carnivory is, in our opinion, not just energy to produce the traps (rudimentary in the case of *Pinguicula*) but an obligation to only live at a place that has sufficient air humidity. The formation of droplets of mucilage indeed results from the existence of holes in the gland cells cuticule (reviewed in Juniper *et al.*, 1989; Legendre, 2000). These cuticular gaps as they are called allow internal plant fluids to freely flow outside. Even though the mucilaginous substances present in the secretions will prevent too much water evaporation, the plant will still dehydrate faster than any other plant in a dry environment. Moreover, we also observed that the plant mucilage is not abundant and sticky enough to retain preys when the air is dry (mid summer and during day time - Tab. 1). This is somewhat in contradiction with a study conducted by Zamora (1995) on *P. vallisneriifolia* which suggested that too high of an air humidity will dilute plant secretions to render them inefficient. But this discrepancy may very well be explained by differences in mucilage composition between these two species and/or wide differences in air humidity between the places where they live.

4- Some normal needs for a green plant

Just like most other plants, the Reims *P. vulgaris* seem to grow better with more light and more water. Similar results have been recently obtained on *P. vallisneriifolia* (Zamora *et al.*, 1998). Moreover, a recent study has suggested that *P. vulgaris* has no specific adaptation to survive very high north or very high on mountains unlike other *Pinguicula* such as *P. villosa* and *P. alpina* respectively (Thoren and Karlsson, 1998).

5- Life is a matter of compromise

Taken together, our observations suggest that *P. vulgaris* will do best in a humid area that has no tall vegetation, a strong light (no sun though), rich soil and a long non-freezing period. These conditions have prevailed in central Europe during and right after the last glaciation period and these must have been good days for this species. However, these days are gone and survival has required a strong sense of adaptation and is a matter of compromise and/or opportunity.

This notion of compromise has already been stated by Zamora (1995) in one of his study which concluded that *Pinguicula* need enough light to survive but not too much to still have enough insects flying around. But it may be extended much further than that.

Arctic regions provide too little sunlight and too short summers (which may at some point not allow a full vegetative cycle), but preys are abundant, humidity is high and neighboring vegetation is small. The same holds true for alpine environments where vegetative periods may be too short but where preys are abundant, light levels and humidity are high and many environments such as cliffs provide room to develop in an open space.

Comparatively, low-land France does not normally provide good places for plant development. On most of the country, air humidity goes too low when temperatures rise and local vegetation is generally too tall to allow a small *Pinguicula* to fight its way through. The rare humid areas are often made of acidic peat bogs which soils are too poor for *P. vulgaris* (it can still be seen, on rare occasions, on such places), but are sometimes generated by alkaline bogs (as in the Champagne area). These later places will provide some unique ecological niches. The plant will be looking for a place that has enough sand to stunt other plants, but that can hold water well with enough clay. A mix of the two at a spring is a perfect place for this. Moreover, the plant will need calcium (see below) and organic food to flow to its roots. This is best obtained when the water that reaches the plant has passed through a rich forest floor beforehand and when some clay, lime or gypsum is present next to the plants. This unique combination of soils ingredients can only be obtained at a junction between different soil layers where some mixing has been obtained over geological ages. Locally, this mixing is favored by the stepping of animals or more recently by the passage of motorcycles which is high at these places since they are located outside the forest areas and above bogs. Let's note that both animal stepping and motorcycles will help trim grasses and scatter the many gemmae produced by winter buds.

6- A potential dual role for a key mineral element, calcium

Calcium is, in our hands, clearly needed to allow survival of *P. vulgaris* in cultivation. This may result from its ability to bride clay and organic matter (pectins) to form an argilo-humic complex. This phenomenon will prevent the soil from becoming too compact (by spacing its fibers) and will favor both root aeration and root penetration (by forming cages). However, in the wild, *P. vulgaris* can be seen on pure peat or acidic soils. This may be explained by the fact that soils tend to compact more in small pots than in nature. Moreover, calcium often comes with alkaline materials (lime, chalk) which do not permit the development of a the phytopathogenic fungus *Pythium* to which the plant seem sensitive and which is common under cultivation and may not exist, for other reasons, in some natural habitats.

7- Where being small may be an advantage

While we have no obvious explanation for the presence of round rather than pear-shaped seed capsules, there may be a reason for the small size of the Reims *P. vulgaris*. A smaller size will indeed limit dehydration in a dry environment and will help hide from the winds and direct sun next to some grass. It also diminishes the likelihood of being stepped over by an animal at a place where they visit very often.

8- A need for the presence of human beings

It is obvious, from all of the places where the Reims *P. vulgaris* grow, that they beficiate to some extent from human activity. They are found in the marks made by trucks, motorcycles or horses.

9- Gloomy future: a call for action

But modern human activity (about 30 years) is also rapidly placing too much pressure on these plants and will rapidly lead to their entire destruction. Most of the wet habitats have been drained and are now cultivated. Horses are no longer used to trim bog weeds which now overgrow the rare *Pinguicula*. But, we feel that there is another more perverse effect.

While observing the 3 sites described above over some years, we witnessed a dramatic reduction in plant number in each site. The number of plants at the Berru site has gone from 2000 to 70 within 4 years. In Chenay, it has gone from 700 to 20 over the same period and from 4000 to 2000 over the past year in Neuf ans. We've been puzzled a long time on the reason behind this extinction. The sites where the plants grow (and their immediate surroundings) have indeed not received any significant change over these years (three growth, farming, clearing…). Our only hypothesis is that the plants slowly dye off because of an overall lowering of the air humidity in the state.

The Champagne state has indeed always been famous for its bogs and dense fogs. Even though some bogs remain, they are small and isolated from each other and the air has dried up irreversibly over the past 20 years because of extensive farming over the state during this period. Foggy days are now rare (Tab. 1).

This leaves no obvious way to protect our favorite plants in their natural habitat. Planting more trees to cut winds and trimming grasses above the plants may actually be the best thing that can be done, the worst action probably being to cut down some of the branches of the trees that surround the plants to give them some extra space because this would lead to higher air movement and thus greater loss of humidity. More rain does not seem to compensate for the low air humidity encountered on some days.

Extinction in the wild seems very close (within the next 5 years?) and we feel that cultivation may be one of the only alternative to prevent total extinction of a plant population which still has so much to teach to us. Cultivating temperate *Pinguicula* is, however, difficult and achieved by only very few persons even though some pioneering efforts have already been published (Steiger, 1975).

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Jan.	Feb.	March	April	Mai	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean daily maximum temperature (°C)											
+2.0	+10.2	+13.3	+14.6	+18.9	+21.2	+23.4	+27.9	+22.1	+15.3	+10.1	+7.3
Absolute temperature maximum (°C)											
+10.2 on 22th	+15.7 on 28th	+19.0 on 12th	+20.3 on 10th	+26.8 on 03th	+27.9 on 10th	+29.1 on 30th	+33.6 on 24th	+27.6 on 18th	+24.5 on 06th	+13.8 on 05th	+14.6 on 25th
Mean daily minimum temperature (°C)											
-4.2	+2.7	+4.4	+1.6	+7.7	+11.5	+11.8	+15.0	+7.8	+5.0	+4.5	+2.8
Absolute temperature minimum (°C)											
-18.3 on 01th	-5.3 on 01th	-2.7 on 22th	-5.5 on 21th	+0.6 on 08th	+4.6 on 01th	+8.2 on 05th	+11.1 on 20th	+1.6 on 22th	-5.0 on 30th	-5.2 on 02th	-4.2 on 06th
Number of frosty days (Tn<=0°C) under cover											
24	6	5	14	0	0	0	0	0	9	3	7
Number of days with ice storms											
0	1	0	0	0	0	0	0	0	0	0	0
Cumulative rain fall (mm)											
6	59	19	19	74	118	68	54	20	49	99	58
Number of rainy days (RR>=0.1 mm)											
8	21	21	7	20	24	19	16	21	22	23	22
Number of fogy days											
8	3	6	0	1	0	8	6	10	7	8	3
Number of snowy days											
6	1	0	1	0	0	0	0	0	0	0	4
Number of days with snow cover											
14	0	0	0	0	0	0	0	0	0	0	4
Quantity of sun received (h)											
63	75	129	226	241	164	233	248	246	164	45	46
Mean relative air humidity (% - obtained with 8 measurements per day) :											
90	84	83	68	78	81	79	76	78	82	90	90
Mean maximum relative air humidity (%)											
96	95	97	92	96	97	98	97	98	96	97	96
Mean minimum relative air humidity (%)											
80	65	59	41	51	54	50	46	47	59	78	79
Number of stormy days											
0	2	0	0	5	9	6	4	1	0	0	0
Maximum wind speed (m/s)											
15 on 22th	32 on 18th	18 on 19th	18 on 20th	23 on 20th	23 on 11th	16 on 12th	15 on 30th	12 on 13th	20 on 09th	20 on 09th	23 on 25th
Mean wind speed (m/s - obtained with 8 measurements per day)											
2.7	5.5	3.2	3.8	3.7	3.5	2.8	2.4	2.2	3.5	3.8	4.8
Number of highly windy days (Vx>=16 m/s)											
0	10	3	3	4	3	1	0	0	5	3	7

Table 1: Weather information taken in 1997 at the meteorological station of Courcy in close proximity of the *P. vulgaris* sites. Elevation 91 m. Origin: Meteo-France.

Figure 1: World distribution of *P. vulgaris*. According to Casper (1966).

Figure 2: Distribution area of *P. vulgaris* in France. Localities described before 1960 are marked by a square. If the plants have not been seen since this date the square is left open (□). It is filled (■) when the presence of the populations has been described again since (Source: Dupont, 1990).

Figure 3: Schematic view of Reims *P. vulgaris* sites. (1) Water infiltrates through a sandy soil layer. (2) Water flows above a Clay-Chalk-black peat soil. Alkaline bog. Tall grasses are present. (3) Place where *P. vulgaris* is found. Water flows out of the ground. Grass is small. The plants are located on a trail. (4) Acidic forest. (5) Organic litter accumulation. (6) Quartz sand layer, 80 cm to several meters thick. (7) Clay-chalk soil layer, 50 cm to 1 m thick. The arrows indicate water flow.

Figure 4: The Reims *P. vulgaris*.

Figure 5: Flower of the Reims *P. vulgaris*. All pictures were taken by L. Legendre except the one showing the round seed caps which was kindly provided by Pr Juerg Steiger.

Figure 6: Electron microscopy pictures of Reims *P. vulgaris* (A,B), alpine (Contamines) *P. vulgaris* (C,D), Iceland *P. vulgaris* (E,F) and *P. mundii* (G,H).

Figure 7: Electron microscope picture of Reims *P. vulgaris* anther (A) and pollen grain (B). Arrows on part A point towards individual pollen grains. The bag-like structures on the pollen grains in B are phenolic secretions that have not been washed off during sample preparation.

Figure 8: Some examples of structures of flower throat hairs of the Reims *P. vulgaris*.

Fig 1.

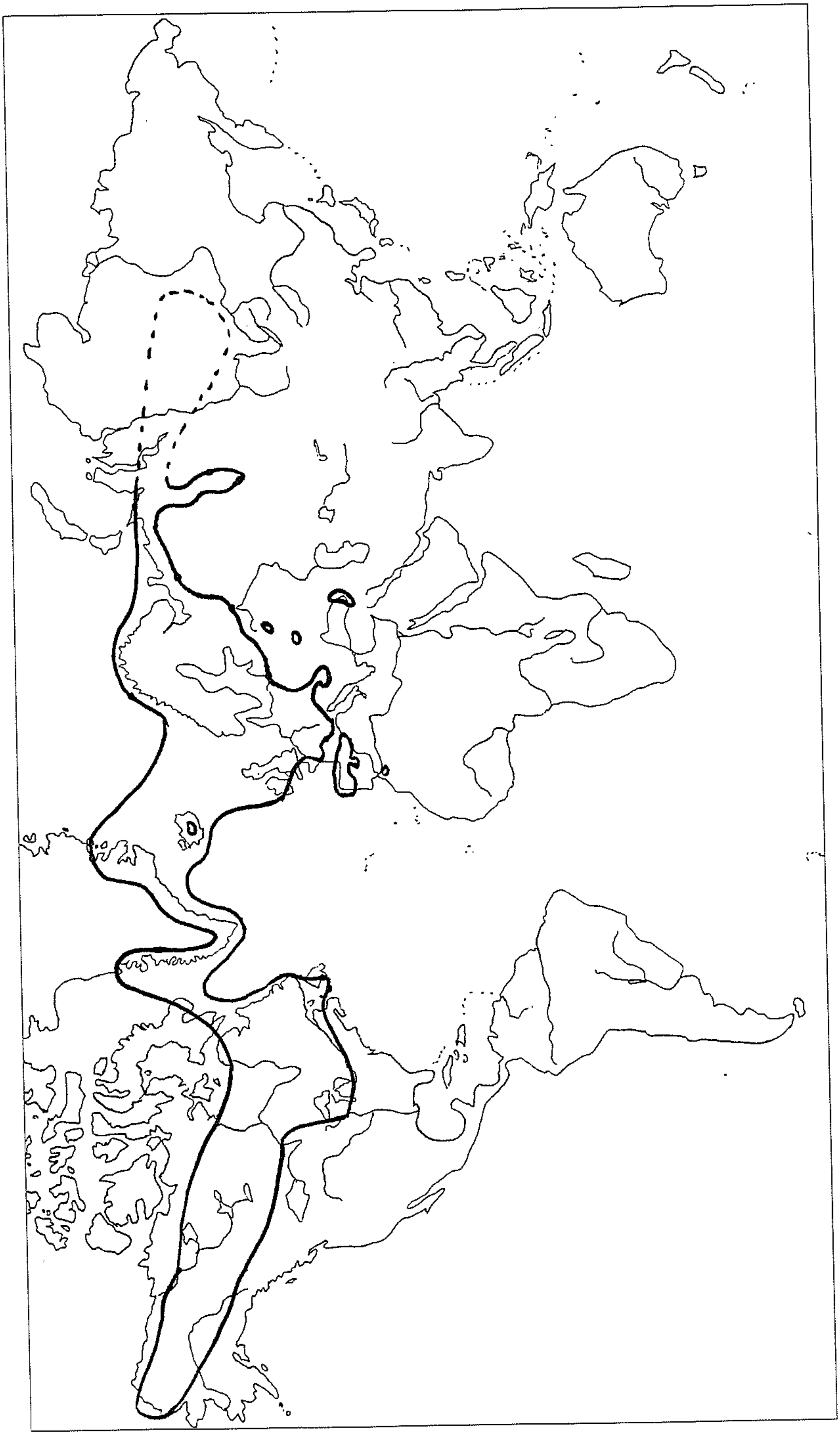


Fig 2

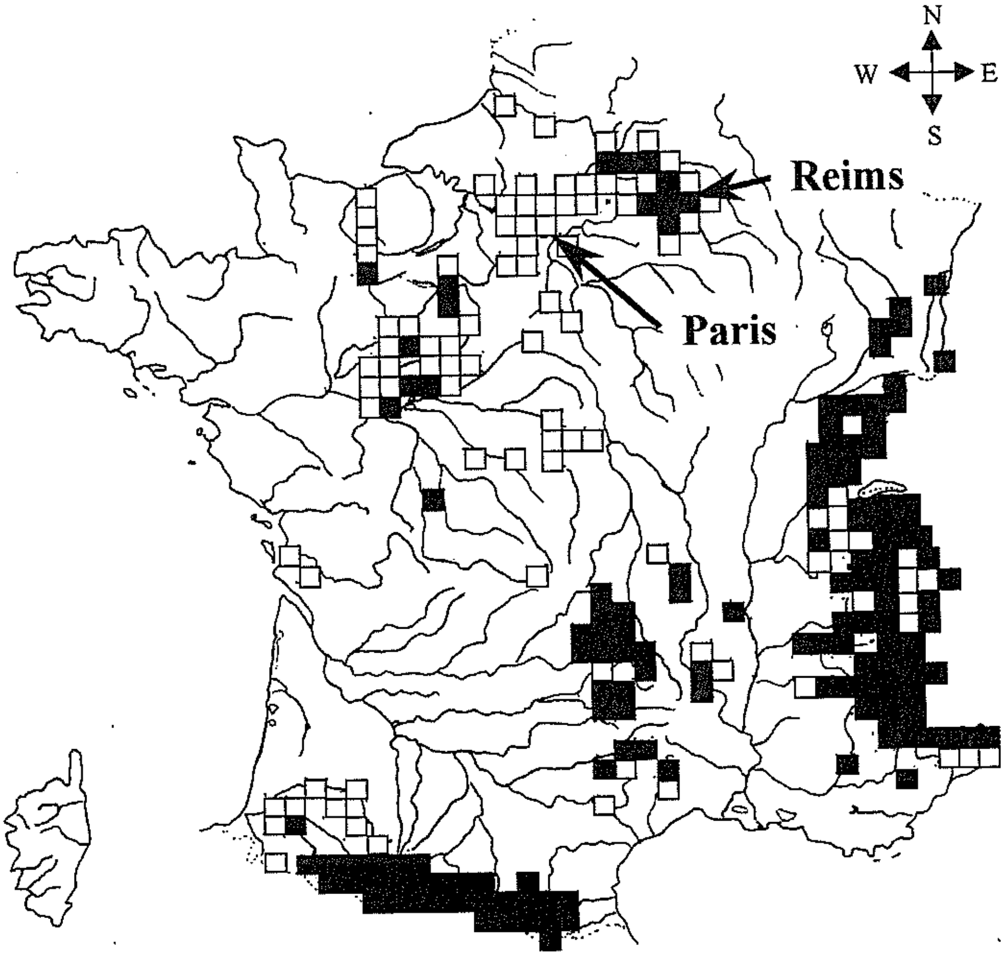


Fig. 3

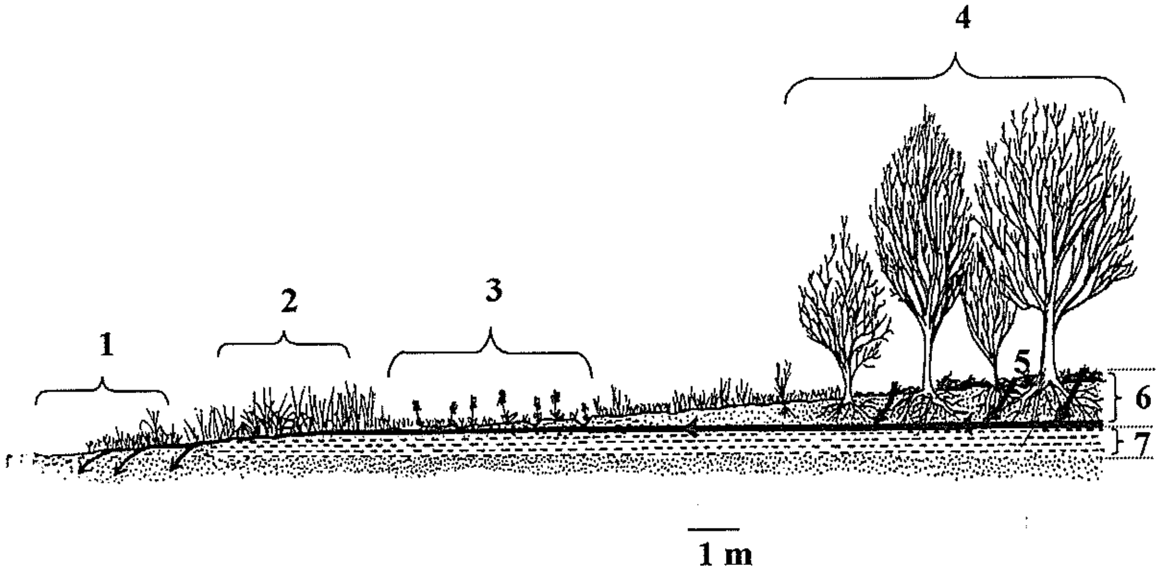
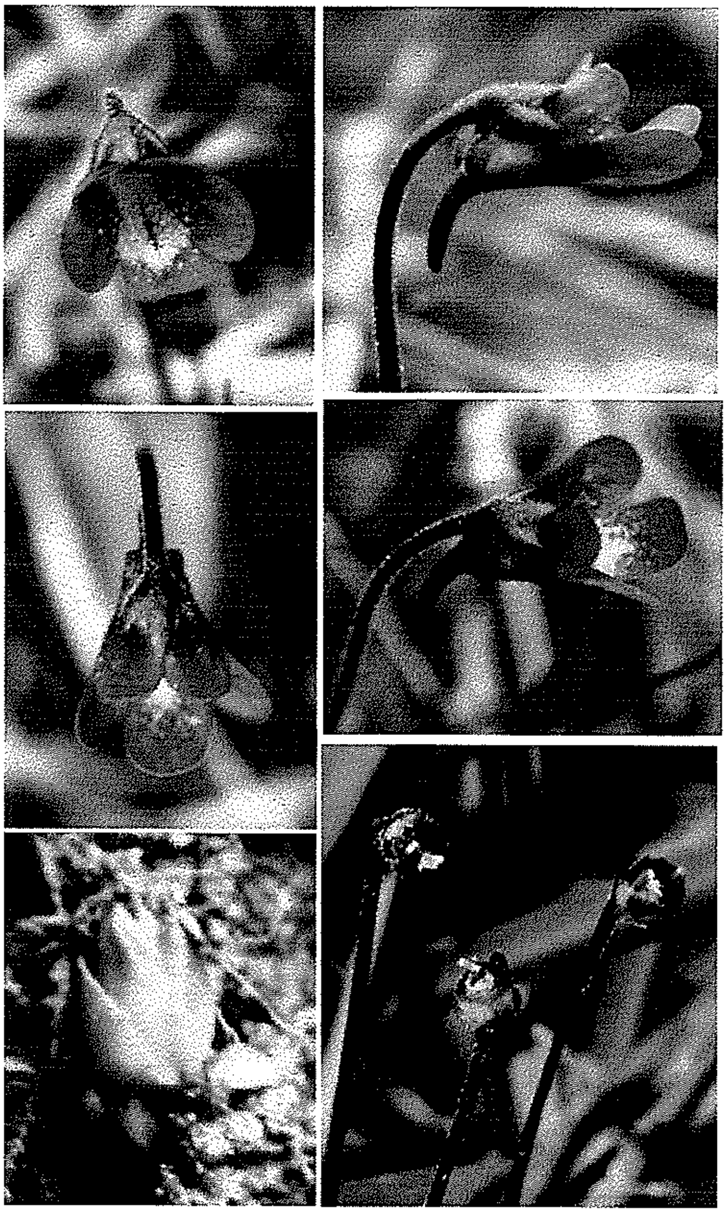


Fig. 4

Fig 5



1 ... Si je mets la main sur un scanner à diapos, je changerai cette dernière photo par une comparaison entre les capsules de Reims et les alpes.

Fig. 6

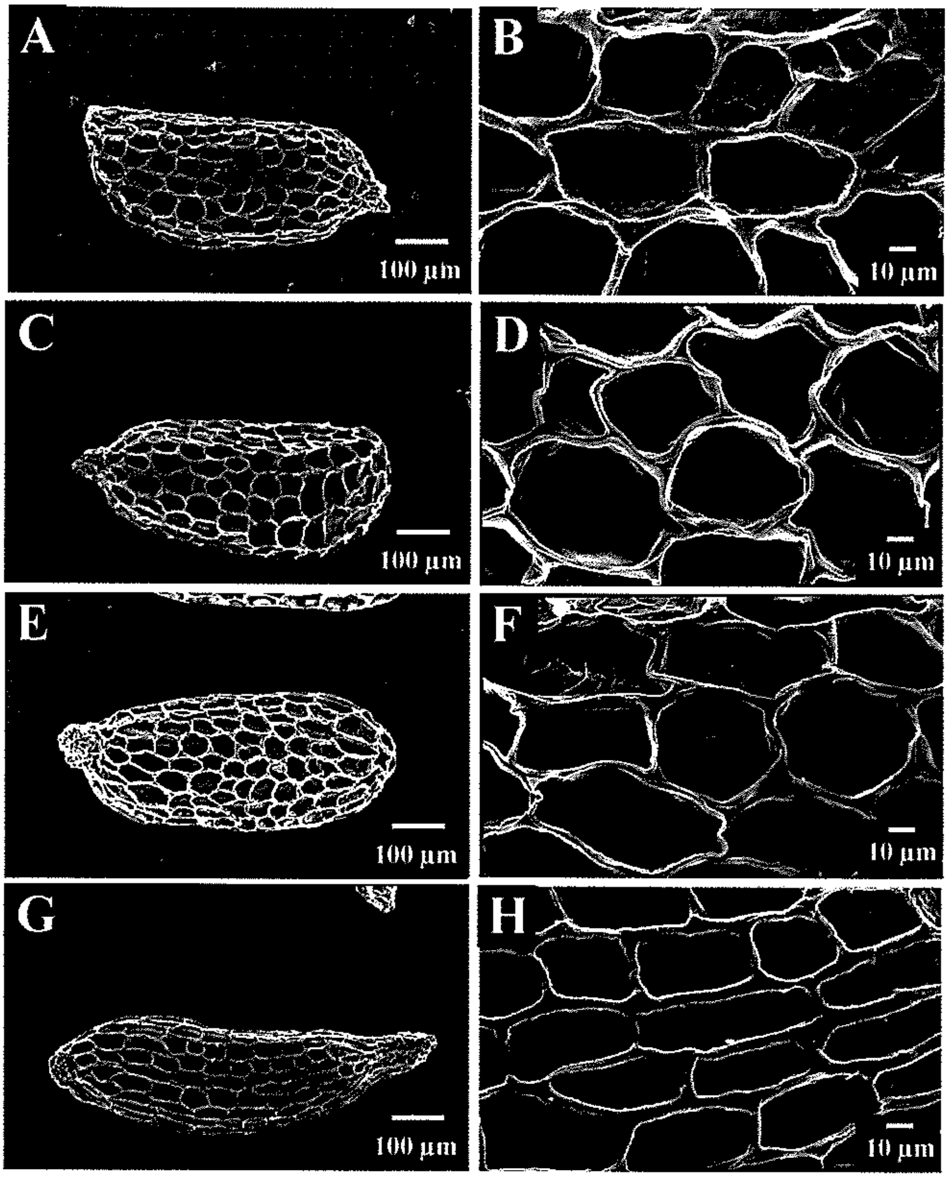


Fig. 7

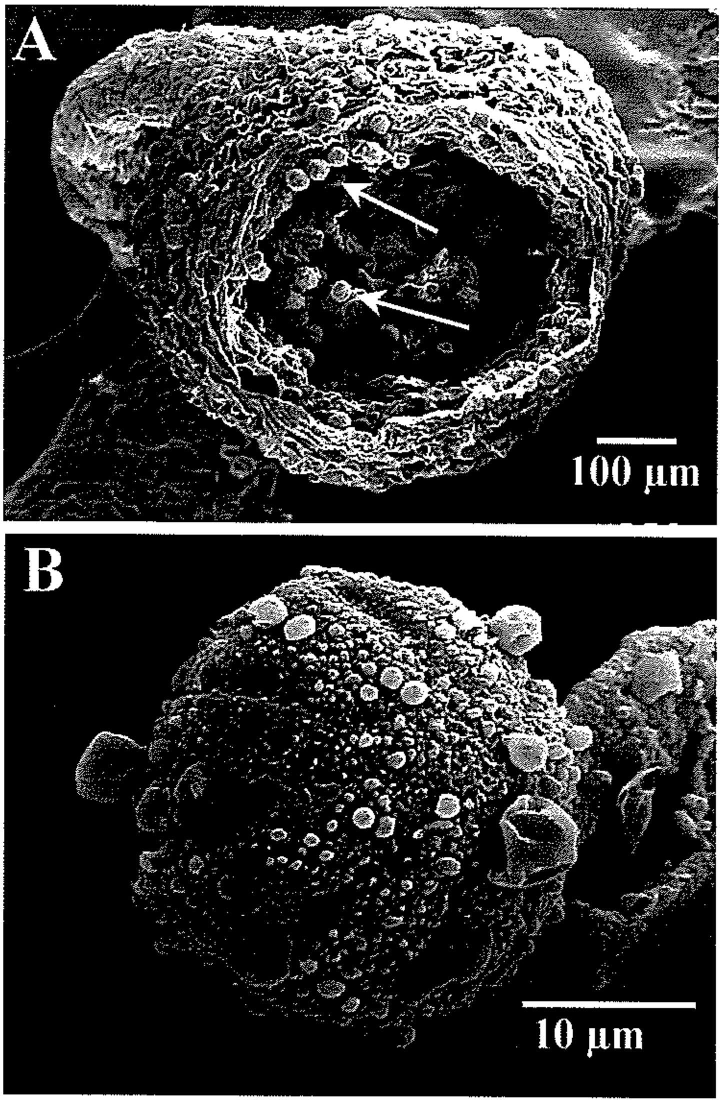


Fig. 8