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LIFE CYCLE VARIATION IN PEDICULARIS PALUSTRIS L. (SCROPHULARIACEAE)

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SUMMARY

Different flowering times of *Pedicularis palustris* ssp. *palustris* (May-July) and *P. palustris* ssp. *opsiantha* (Ekm.) Almquist (July - September) are related to variation of the life cycle: ssp. *palustris* is a biennial, ssp. *opsiantha* is a summer annual. Growth experiments confirmed the genetic basis of the difference. The biennial has rosette leaves in the first year, and forms a winter bud with scale-like leaves. These leaves or their scars are visible in the flowering plant; they are missing from the annuals. Germination requirements are similar; fresh seeds germinate at rather high temperatures (25–30 °C) only, but stratification widens this range. The adaptive nature of the life form is discussed in relation with the different habitats in which the taxa are found.

1. INTRODUCTION

According to HEUKELS & VAN OOSTSTROOM (1973 and earlier editions) the hemiparasite *Pedicularis palustris L.* (Scrophulariaceae) is a biennial, flowering May-July. In 1971 plants flowering late summer were found in some areas along the western coast of the Dutch province of Friesland (TER BORG & KOEMAN-KWAK 1973; HEUKELS & VAN OOSTSTROOM 1975 and later editions). This observation led to a further study of the intraspecific variation of this species.

Literature on late flowering *Pedicularis palustris* stems from two groups of authors, Scandinavian and French, who seem to have been unaware of each other. In Scandinavia the first major paper came from EKMAN (1909) who described the late flowering *P. opsiantha* Ekm. from S. Sweden; later JOHANSSON (1916) and TUOMIKOSKI (1936) reported on plants from Gotland and Karelia. The late plants are more slender, their leaves more dissected and their flowers somewhat smaller than those of the early flowering group. With respect to habit and branching the authors seem to disagree slightly (*table 1*). According to HARTL (1974) the late flowering taxon, *P. palustris* ssp. *opsiantha* (Ekm.) Almquist, is restricted to Scandinavia and the extreme Northern parts of Germany; the early flowering *P. palustris* ssp. *palustris* is found all over Europe except for the South, and in some places in Eastern N. America.

SQUIVET DE CARONDELET (1955) described the late flowering *P. palustris* spp. *serotina* Sq. de C., from marshes in the Rhône delta. His plants were also slender and had finely dissected leaves, and in addition he found they were annuals. According to him and to WATTEZ (1974) 'late' populations are rare outside the Mediterranean area, but widely scattered: from the Channel coast to S. France, N. Italy and the Alps.

This paper compares the life cycle and the habitat of early and late flowering populations of *P. palustris* in the Northern Netherlands, and discusses the infraspecific variation of the species.

2. OBSERVATIONS

2.1. Population data

The late flowering populations in Friesland were found in three nature reserves: Bocht van Molkwerum, Piamer Kooiwaard and Makkumer Noordwaard. They were compared with early flowering populations in the Makkumer Noordwaard

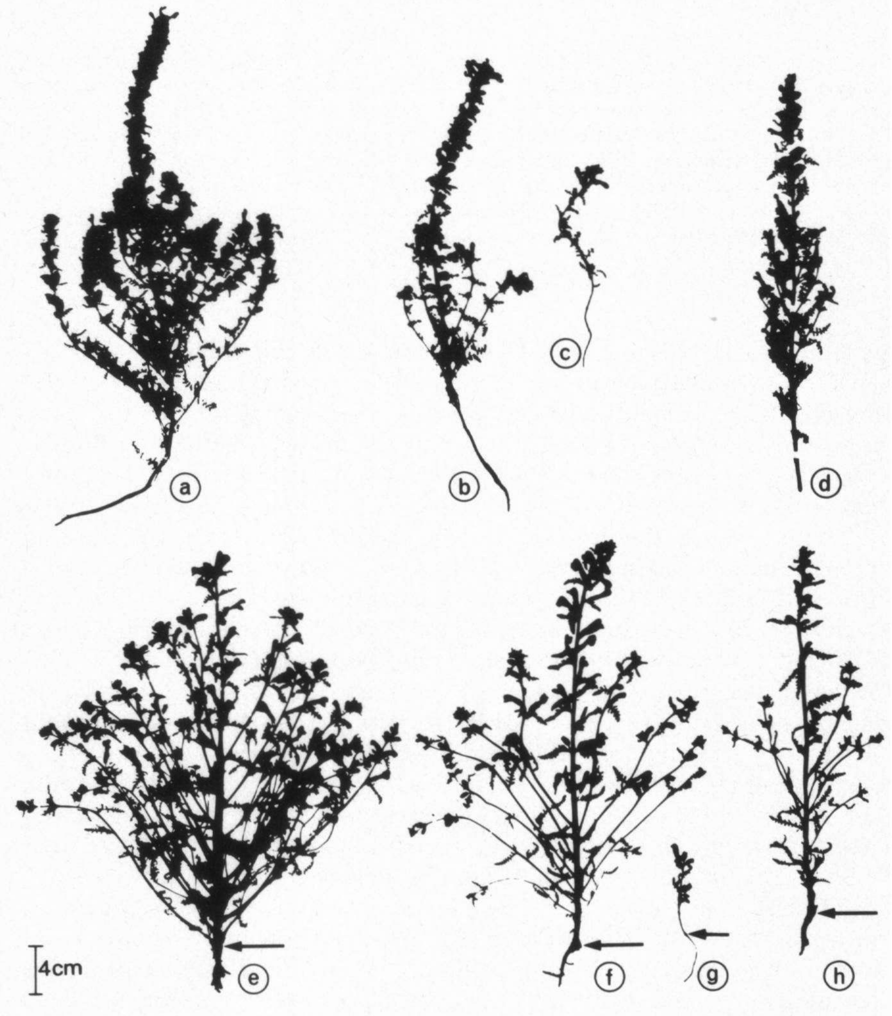

Fig. 1. Variation in annuals (a-c) and biennials (e-h); d: type-plant of *Pedicularis palustris* L. ssp. *opsiantha* (Ekm.) Almquist (Ekman, Herb. Lund). Arrows indicate scars and remnants of winter bud.

and elsewhere in the Northern part of The Netherlands.

Field observations at various times of the year indicated that the late plants are summer annuals, whereas the early flowering ones normally have a biennial life cycle. Both types germinate in April-May. The annuals flower from late July until September and complete the life cycle in September-October. The biennials form rosette leaves in the first year and a thick root, full of starch; after the formation of a winter bud covered with scales the leaves dehisce. Growth starts again in March, the plants flower from mid-May onwards, and set seed in June-July. The two forms could be easily distinguished in most cases, since in the biennials either the rosette leaves or the winter bud, its scales or their scars (up to c. 20) are usually clearly visible. In annuals the number of leaves or scars at the stem basis is rarely over 10. In some rare cases aberrant life histories were observed in the biennials. These included mass germination in summer, and, on another occasion, outgrowth of winter buds in autumn, followed by formation of new buds in the axils of the young leaves. *Fig. 1* illustrates the variability and similarity of the habits of both types; other morphological characters are summarized in *table 1*. The table indicates that late Dutch plants differ slightly from

Table 1. Review of characters of *Pedicularis palustris* ssp. *palustris* and ssp. *opsiantha*.

	ssp. palustris (early)	ssp. opsiantha (late)	plants from Frisian coast (late)
habitus	robust	slender	slender
stem	herbaceous flexible thicker	woody brittle relatively thin	herbaceous flexible relatively thin
branches	from the basis; straight or curved	from mid stem and higher; straight or curved (Ekman) from the basis (Tuomikoski)	from the basis or higher; straight
leaves	less dissected	more dissected	more dissected
width of midrib	c. 2mm	c. 1 mm	c. 1 mm
intercalary leaves	none	1 or more (Ekman) none (Tuomikoski)	none
part of main stem with flowers	> ½	up to ¼	up to ⅓
calyx	not inflated	inflated (Ekman) not inflated (Tuomikoski)	not inflated
flowers	18–20 mm	14–17 mm	18–20 mm (in local early plants > 20 mm)
life form	biennial	? (Scandinavian) annual (French)	annual
flowering time	V–VII	VII–IX	VII–IX

late ones elsewhere.

In the Rijksherbarium (Leiden) we did not find any specimens of late flowering populations, neither recent nor old ones. During a visit to Britain we found both types, the biennial in a small marsh near Oxford, the annual in moist sites of a grazed area near Hungerford (Berks.).

2.2. Growth and germination experiments

Comparative growth experiments were performed by growing plants from seeds, both outside – at the edge of a pond in the experimental garden in Haren – and in pots in a greenhouse, with and without hosts (*Agrostis* spec.). It turned out that the life cycle difference is genetically determined. Seeds from annual plants again produced annuals. The life history of the biennials appeared to be affected to some extent by the growth conditions, which apparently keep it in phase with seasonal variation. Details on this subject will be published elsewhere.

To test germination requirements seeds were placed in petri dishes on moist filter paper at various constant temperatures in LD 12 : 12. It was found that fresh seeds of both types germinate best at high temperatures (*fig. 2a*). After stratification (seeds kept moist at 4 °C) germination occurred over a wider range of temperatures (*fig. 2b*). Final percentages were usually reached within a couple of weeks, except for untreated samples at lower temperatures, where germination continued for several months. Further experiments showed that variable temperatures had no particular stimulating effect.

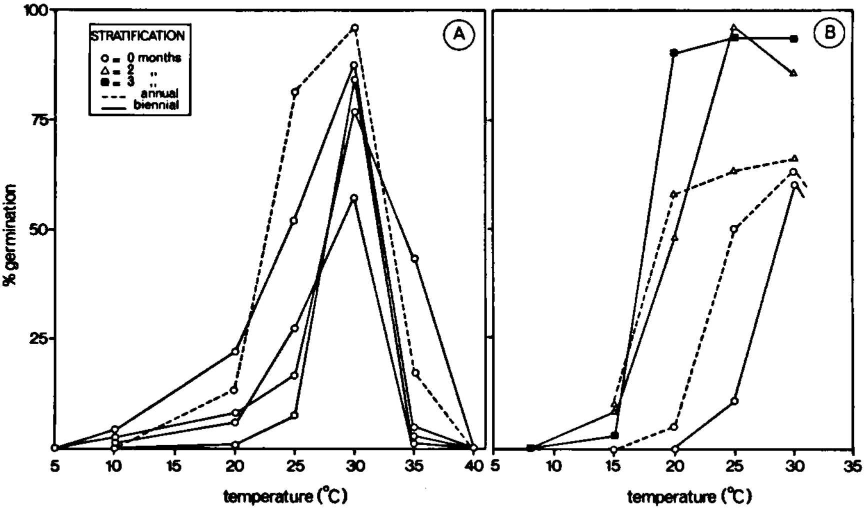

Fig. 2. Germination percentages at various constant temperatures. A: fresh seeds; B: after various periods of stratification.

2.3. The habitat

The nature reserves outside the Frisian west coast with late flowering plants originally were bare sand flats in the former Zuiderzee, flooded tidally with brackish water (FEEKES 1943). After the closure of the "Afsluitdijk" (1932) the sand flats emerged and gradually desalinated. Today they are only incidentally inundated by fresh water. The vegetation which developed is still gradually changing. In some areas it is mown or grazed by cattle. High reeds and *Salix* shrubs grow in some places, *P. palustris* is found in relatively low and open stands of grasses and dicots.

The early flowering populations in the Northern Netherlands occur in meadows in marsh areas with peaty soils and a high water table, often inundated in winter and occasionally also in summer (cf. BOEDELTJE & BAKKER 1980). They are mown around mid-summer but in some years this is impossible due to the high water level. Early flowering populations were also found in wet parts of the dune systems of W. Frisian islands.

Table 2 summarizes the vegetation data. It includes the species occurring in all three areas studied as well as those occurring in at least 40–60 % of the relevees in one of the areas (frequency III or more). Moreover the table presents the phytosociological spectra, calculated over species presences. The phytosociological classification is based on ARNOLDS & VAN DER MEIJDEN (1976), with slight modifications; nomenclature of phanerogams follows HEUKELS & VAN OOSTSTROOM (1977).

We conclude from *table 2* that there is a wide overlap in the species composition of the three sets of data. The habitat of the annuals differ by a higher proportion of taxa of the *Agropyro-Rumicion crispi*; the habitat of the biennials is characterized by the presence of more taxa of the *Parvocaricetea* and other marsh vegetation types. This indicates relatively more dynamic conditions for the former and less disturbance and a constantly wet or moist situation for the latter. The nutrient status is probably highest in the marshy meadows.

3. DISCUSSION

First the question arose to which taxon, either the Scandinavian or the French, our material belongs. The Scandinavian papers do not allow a conclusion about the life form of the late plants described. Therefore the "*opsiantha*" material from the herbaria at Lund, Stockholm and Helsinki was studied, including specimens collected and identified by Ekman, Johansson and Tuomikoski. Since the majority of them have no remnants of a winter bud and a low number of leaf scars at the stem basis they must be annuals, including the type-plant (collected by E. L. Ekman, Aug. 1908, in *Sphagnum* bog near Jönköping, prov. Småland. Herb. Lund). There seem to be no other discriminating characters. Hence, there is no reason to consider the late flowering plants from N. and S. Europe to belong to separate taxa. Both the late Dutch and British plants can be reckoned to belong to *Pediculäris palustris* ssp. *opsiantha*, which appears to occur over a much wider range than was formerly thought.

Table 2. Compiled vegetation data from three areas: along the West coast of Friesland (original data), Schiermonnikoog dune valleys (De Noo 1973) and marshy meadows along the Drentsche A (Boedeltje 1976). Species arranged according to a phytosociological classification. Species frequencies (Roman numerals) and percentages of phytosociological spectra. –: species or syntaxon not observed.

Area:	Frl.	Schier.	Dr. A
Pedicularis palustris	late	early	early
No. of relevees	10	92	9
PARVOCARICETEA	10.0	18.1	26.4
– Ranunculus flammula	III	IV	V
– Hydrocotyle vulgaris	IV	V	III
– Epilobium palustre	II	I	II
– Stellaria palustris	II	–	IV
– Carex nigra	–	V	V
– C. rostrata	–	–	IV
– Menyanthes trifoliata	–	–	III
AGROPYRO-RUMICION CRISPI	23.7	15.4	12.4
– Juncus articulatus	IV	IV	–
– Potentilla anserina	IV	III	I
– Trifolium repens	II	I	IV
– Agrostis stolonifera	III	V	V
– Eleocharis palustris ssp. uniglumis	V	IV	II
– Ranunculus repens	IV	–	V
PHRAGMITETEA	27.0	19.3	28.1
– Oenanthe fistulosa	III	–	–
– Lycopus europaeus	III	II	–
– Phragmites australis	V	IV	–
– Scirpus lacustris ssp. glaucus	III	II	–
– Mentha aquatica	V	V	IV
– Galium palustre	IV	V	V
– Calamagrostis canescens	I	I	V
– Iris pseudacorus	III	–	I
– Equisetum fluviatile	–	II	V
– Carex aquatilis	–	–	V
– C. hudsonii	–	–	IV
– Phalaris arundinacea	–	–	IV
WET AND DRY HEATHS, CALCAREOUS MARSHES	1.5	19.6	2.2
– Carex panicea	–	III	–
– Salix repens	–	IV	–
MOLINIO-ARRHENATHERETEA	19.1	12.1	22.6
– Cardamine pratensis	IV	IV	V
– Festuca rubra	II	I	IV
– Holcus lanatus	III	II	I
– Lychnis flos-cuculi	II	I	V
– Poa trivialis	III	–	V
– Rumex acetosa	II	–	V
– Filipendula ulmaria	–	–	IV
– Lythrum salicaria	–	–	IV
– Caltha palustris	–	–	IV
HIGH SALT MARSH	6.3	2.2	–
– Juncus gerardii	III	II	–
FESTUCO-SEDETALIA	1.5	4.5	1.7
RUDERALS IN WET SITES	4.1	0.1	5.6
REST	6.6	8.6	–

The study of the herbarium material showed that the N. Scandinavian *P. palustris* ssp. *borealis* (Zett.) Hultén and *P. palustris* f. *serotina* Neum. collected from Gotland by Johansson have winter buds, and hence at least in the majority of cases are biennials, similar to *P. palustris* ssp. *palustris*. With respect to the latter HARTL (1974) mentioned the occurrence of repeatedly flowering perennials. In our populations we never observed this phenomenon.

When using the term "autumnals" for the late flowering plants, as it is done by e.g. EKMAN (1909) and HARTL (1974), it should be realised that the variation in *P. palustris* is totally different from the seasonal dimorphism observed in other Rhinanthoideae (e.g. *Euphrasia*, *Rhinanthus*, WETTSTEIN 1901). In *P. palustris* the variation is related to a difference in life forms, while in the other taxa it is based on the variation of flowering time within the same life form. The latter allows a wide range of variation with respect to flowering time, habit and other characters (TER BORG 1972, KARLSSON 1974). Possibly the variation observed within ssp. *opsiantha* (*fig. 1* and *table 1*) has a similar basis.

With respect to the adaptive meaning of habitat segregation among annuals and biennials we can only suggest some hypotheses. It is easy to see why the annuals cannot survive in the marshy meadows with biennials. Since they require about five months of undisturbed growth the summer mowing prevents seed production. An occasional cold and wet spring with late inundation postponing germination may limit the period for completion of the life cycle even more. On the other hand, it may be significant that the habitat of the biennials is constantly moist and – at least in the marshy meadows – has a higher nutrient status, thus providing better growth conditions for *P. palustris* than the annuals' habitat. The worse growth conditions of the latter may be fatal for the biennials, since it was found that a small overwintering rosette of *P. palustris* dies. Unlike other "biennial" species it does not continue growth to be able to flower in a later year (TER BORG 1979). It is a matter of opportunity and risk – opportunity to reach a certain minimum size needed for seed production, and risk of mortality during various phases of the life cycle –, whether a species should adhere to an annual, a biennial or a perennial life form (HART 1977). Therefore demographic data allowing quantitative comparison of life histories of both taxa in different habitats might present some further clues (CASWELL & WERNER 1978).

A study of the effects of many environmental factors is complicated by the parasitism of the species, but no host is needed for germination. With respect to its temperature requirements the differences between the taxa appeared to be negligible. Surprisingly, no strict stratification requirement was found, in contrast with other N. European hemiparasitic annuals (e.g. *Rhinanthus*: VALLANCE 1952, TER BORG 1972; *Odontites*: CHANCELLOR 1973; *Melampyrum*: OESAU 1975, MASSELINK 1980).

Populations of the annual ssp. *opsiantha* appear to be rare and scattered. SQUIVET DE CARONDELET (1955) suggested that migrating birds might transport the seeds. If this is true, birds will have a hard job in future maintaining the declining taxon. Of the three populations known to us, two have become extinct in recent years; the same holds for a population in N. France (WATTEZ in litt.).

Another possibility is that the annual populations are polytopic in origin. The variability of the life cycle of the biennials, to be discussed in more detail in a separate paper, suggests that only little genetic change is needed for the development of a summer annual genotype. Therefore a polytopic origin seems a reasonable explanation for the scattered distribution of the annuals. The strong reduction of the habitat of the biennials and their resulting decrease (HARTL 1974) reduces the chance of occurrence of such a process. *P. palustris* ssp. *opsiantha* therefore can be regarded as an endangered taxon; thus far it has received too little attention.

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