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BIOSYSTEMATIC STUDIES OF THE CAREX FLAVA COMPLEX I. FLOWERING

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SUMMARY

As a part of a broader biosystematic analysis of the NW-European species of the *Carex flava* complex a comparative study was made of the flowering of *C. flava*, *C. lepidocarpa*, *C. demissa* and the subspecies *serotina* and *pulchella* of *C. serotina*. In these taxa the inflorescence develops in the same way, except the apical male spike, which in *C. flava* starts anthesis in its lower portion, but in all other species in the distal portion during the principal flowering period and at the other end during protracted flowering. The inflorescence is protogynous. A male spike contains florets in anthesis for several days, each individual floret coming in anthesis for one day only and producing pollen during the morning. A female floret may be in anthesis for several days. The development of the spikes in an inflorescence proceeds basipetally, but anthesis in a female spike proceeds acropetally. The development of inflorescences with an anomalous distribution of the sexes, and the flowering phenomena characteristic of hybrids are discussed separately. The flowering periods of the taxa coincide to an appreciable extent, so that hybridisation is likely to occur.

Protracted or second flowering has only been observed in *C. demissa* and *C. serotina*. Only *C. serotina* comes into flower in the first growing season. The differences between its phenology and that of the other species may be attributable to its specific habitat. All species are anemophilous and exhibit both autogamy and outbreeding.

1. INTRODUCTION

Within the genus *Carex* the *C. flava* complex, belonging to the section *Extensae* of the subgenus *Carex*, is one of the most critical groups. In the present investigation only the NW-European representatives were studied, viz. *C. flava* L. sensu stricto, *C. lepidocarpa* Tausch, *C. demissa* Hornem., *C. serotina* Mérat ssp. *serotina* and ssp. *pulchella* (Lönnr.) Van Ooststr., in the circumscription and nomenclature of KERN & REICHGELT (1954). Since *C. flava* is very rare in the Netherlands and *C. lepidocarpa* does not occur there at all, the study could of necessity not be restricted to this country (see *fig. 1*).

The complex was studied morphologically and karyogenetically by DAVIES (1953, 1955) who used mainly British material, morphologically by PATZKE & PODLECH (1960) in Germany, and both ecologically and morphologically by COESEL (1968) in several European countries. Chromosome counts were reported by several workers (see DAVIES 1955), and the incidence of interspecific hybrids in several publications including local floras, see, e.g., REITER (1950), KERN & REICHGELT (1954), DAVIES (1955), DIETRICH (1964), JERMY & TUTIN (1968), ROTHMALER (1970). The outcome of these studies indicates that the recognition of the above mentioned taxa seems to be the best solution, although the species cannot always be separated with certainty.

The present report is the first of a series dealing with the biosystematics of the group with the ultimate purpose of explaining why, although the segregation of the taxa within the complex is not always clear, several taxonomic units can be accepted. Subsequent publications will treat the chromosome numbers, the degree of possible hybridisation, the habitat ecology, and the morphological features.

In view of a possible genetic isolation of the subordinate taxa of the complex, the following questions concerning flowering are relevant:

1. Do the taxa studied differ in their mode of flowering?
2. Are there any differences in the flowering periods?
3. What pollination strategies occur?

The answer to the first question may conceivably also contribute new diagnostic characters to segregate the taxa.

2. LITERATURE SURVEY

Judging by the limited space in anthecological publications (see, e.g., FAEGRI & VAN DER PIJL 1971, KNUTH 1899, KUGLER 1970, LOEW 1895, PROCTOR & YEO 1973) devoted to the flowering and pollination ecology of Cyperaceae, these subjects are poorly known. Loew and Knuth report that protogyny is of general occurrence among the sedges; Knuth and Proctor & Yeo record incidental observations of pollen-consuming insects on *Carex* inflorescences (confirmed by unpublished observations by Meeuse and collaborators). All anthecologists state that *Carex* is typically anemogamous. PONOMAREV & PODOSENOVA (1974) reported that *Carex* and some other Cyperaceae only produce pollen in the morning. Floras usually mention varying flowering periods of the *Carex* taxa concerned, compare the discussion.

According to EAST (1940) Cyperaceae are self-fertile. FAULKNER (1970) states that the section *Acutae* of *Carex* (not closely related to the *C. flava* complex) is but little self-compatible.

3. MATERIAL AND METHODS

The starting point of all investigations was the local population, for the present study defined as the total of all individuals found simultaneously at a certain site and morphologically forming a continuum. The populations were identified by means of the characteristics used by KERN & REICHGELT (1954), and coded by a locality number and a letter as follows: F stands for *C. flava*, L for *C. lepidocarpa*, D for *C. demissa*, S for *C. serotina* ssp. *serotina*, and P for *C. serotina* ssp. *pulchella*.

In a number of sites more than one species of the complex may occur. They differ in their microhabitats, however, although a small overlap is not infrequent. The species under discussion have become rarer in the last century (see ARNOLDS & VAN DER MEYDEN 1976), and have disappeared in many localities mentioned in publications that appeared after 1945. Relevant data were ob-

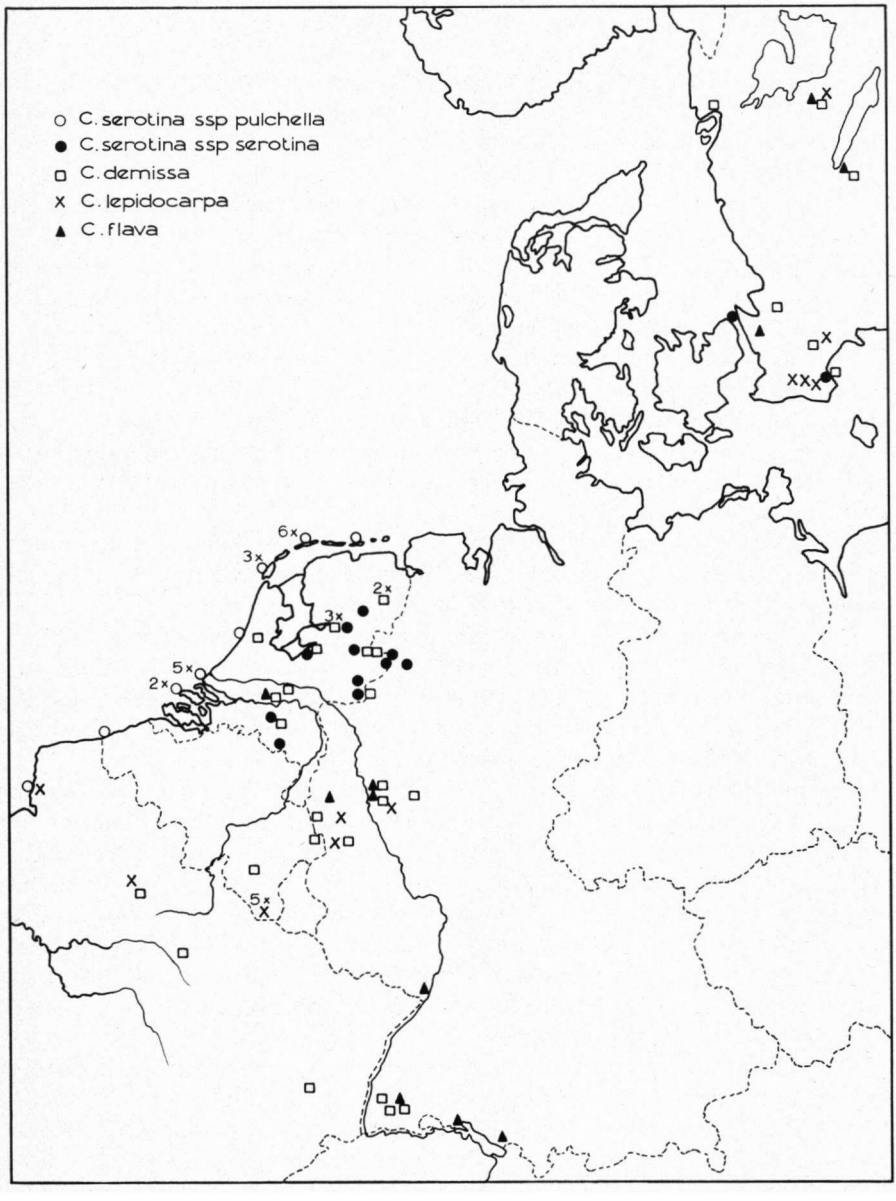

Fig. 1. Distribution map of populations of which the flowering phenology has been studied in the experimental garden.

tained from the Rijksinstituut voor Natuurbeheer (R.I.N.), Leersum; from the Rijksherbarium, Leiden; from Mr. G. Visser (Biological Field Station, Terschelling) and from Mr. P. F. M. Coesel (Hugo de Vries laboratorium, Amsterdam). Localities of populations outside the Netherlands were kindly supplied by the Botanic Institute, Lund (Sweden) and by Dr. E. Patzke, Aachen (W. Germany).

In the experimental garden of our laboratory phenological observations were recorded of plants hailing from 42 Dutch and 49 foreign populations (see *fig. 1*), which plants were either transplants of 5–15 specimens or raised from seed. The transplantations had taken place at least as early as the summer before to up to a year before the flowering was described.

The material used did not only differ in geographical origin but also in ecological background (see the indications of the growing sites in KERN & REICHGELT 1954, ROTHMALER 1970, and WESTHOFF & DEN HELD 1969).

Only those observations were used which were made of plants that appeared to bear well-developed fruits. The flowering of artificial and natural hybrids will be treated separately (see p. 10).

For practical reasons the recording took place in the experimental garden from 1971 till 1976, but the dates were augmented by incidental phenological studies in the field from 1971 till 1973, which were concurrent.

The development in culture was followed by the daily recording of labelled flowering scapes, 487 in all and obtained from 35 wild populations. Additional observations were made of all transplants and of all plants raised from seed. The sequence of development was described by noting the positions of the wilted florets, florets in anthesis and unopened florets within the inflorescence.

The flowering period was recorded by studying three different series of plants, each reared simultaneously and grown under the same conditions. Plants of the first series were grown in a plastic container 45 cm × 30 cm × 8 cm; the plants of series 2 and 3 individually in earthenware pots of 12 cm diam. Series 1 contained 28 population samples of 36 of 54 specimens each, which produced 0–10 inflorescences per plant; series 2 and 3 contained 9 and 5 population samples, respectively, of 4–51 specimens each, which produced 20 or more inflorescences per plant. Series 1 and 2 consisted of plants raised from systematically collected seeds samples of natural populations.

The plants of series 3 originated during hybridisation-experiments after selfing or after outbreeding with a different plant of the same population.

As a measure of the progression of flowering per plant the number of terminal male spikes containing one or more florets in anthesis were counted daily. The temperature registration took place by the 'Nautisch en Weerkundig Instituut' (Amsterdam) in a standard weather hut in the adjoining Botanical Garden.

4. DEVELOPMENT OF THE INFLORESCENCE

4.1 Structure of the inflorescence

There is some controversy as regards the interpretation of the 'flower' and the

'inflorescence' in *Carex* and in Cyperaceae generally. (For the conventional interpretation, see, e.g., VON WETTSTEIN 1935 and FIRBAS 1962, for criticism and alternative ideas, SCHULZE-MOTEL 1959, KERN 1962, MEEUSE 1975, and SMITH & FAULKNER 1976). For this reason the present author chose, for convenience, a certain terminology which does not imply that he endorses one of the opinions.

The term *inflorescence* will be used for the total, complex floral aggregate consisting of a culm emerging from the rosette of leaves with all attached spikes and bracts. In the *Carex flava* complex it usually has the following construction (see *fig. 2*): The apex is formed by a *male spike* below which (1–) 2–3 (–5) more or less crowded, *female spikes* are found, the lowermost one of which may be inserted much lower, near the middle of the culm or even below it.

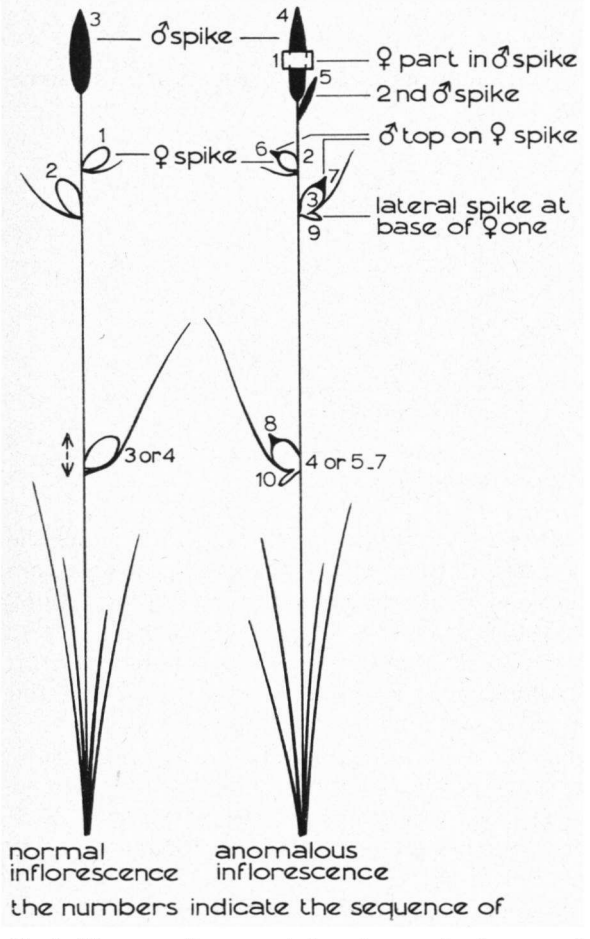

Fig. 2. Diagrammatic representation of a normal and an anomalous inflorescence of *Carex flava s.l.* If the same number appears twice in the same figure it means that spikes with the same number (may) flower simultaneously.

The *male spike* consists of an axis with scaly bracts each subtending 3 stamens constituting what will be called here the (naked) *male floret*. The *female spikes* are subtended by a foliaceous bract and consist of an axis bearing scaly bracts with in the axil of each bract a naked pistil surrounded by a utricle. Anatomical and comparative studies by BARNARD (1957), SCHULTZE-MOTEL (1959), SNELL (1936) and SMITH (1966) indicate that the utricle represents a modified bract of a higher order subtending a naked female floret. The original axis, of which the utricle is the prophyll, is not developed in *Carex* as a rule. The seemingly terminal female flower with sympetalous perianth is in fact a reduced spikelet with a single, laterally inserted female floret and the female spike a compound spike. The *female spikelet* is here defined as the utricle with its *female floret* and the latter consisting of the pistil only.

4.2 The female spikelet

The female spikelet develops in the same way in all five taxa studied, as diagrammatically is shown in *fig. 3*.

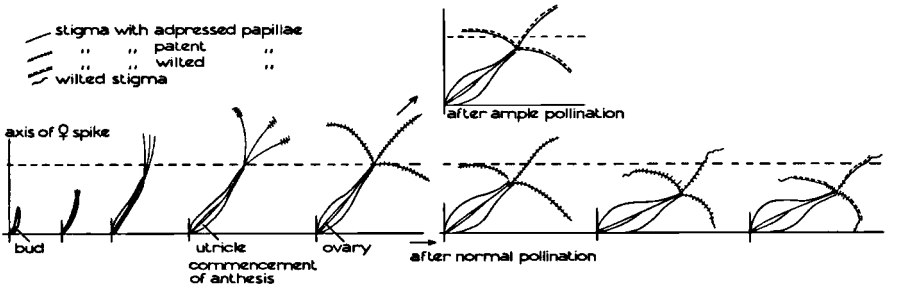

Fig. 3. Diagram of the development of the female spikelet.

After the gradual protrusion of the stigmas (which may take from 1 to 3 days) the stigmatic papillae become erect starting from the top. The stigmas diverge from one another and assume a shiny and bright, white appearance. This initiates the anthesis. During the first one to two days of anthesis the stigmas elongate somewhat and spread out a bit more. During the last one to two days their tips may already start wilting; the wilting proceeds in the same sequence as the raising of the papillae. As a rule the lowermost papillae wilt one to two days later than the uppermost ones. After ample pollination of a female floret all papillae wilt in a day, although unpollinated florets in the same spike may still be in anthesis. When not pollinated, the papillae wilt very gradually. The termination of the anthesis cannot be determined with a greater accuracy than about a day. Anthesis lasts for 2 to 9 days dependent on the weather and on the rate of pollination. Between the five taxa no significant differences were noticed. During anthesis till shortly afterwards the utricle enlarges and becomes more patent (see *fig. 3*). This enlargement starts earlier and goes to a greater extent than is needed for the developing fruit.

4.3 The female spike

The female spike develops in the same way in all five taxa studied, viz., acropetally; the lower florets start anthesis one day or less earlier than the apical ones. For this reason differences in anthesis are often not conspicuous within the same spike (see *photos 1* and *2*). The sequence of wilting is the same as that of anthesis, the amply pollinated florets, which wilt sooner, excepted (see above).

Anthesis commences in the middle or uppermost part in spikes which have been surrounded by the sheath of the bract for a long time; this only occurs in the lowermost spikes because the upper bracts have but a short sheath.

4.4 The male floret

The male floret develops in the same way in all taxa studied as shown diagramatically in *fig. 4*.

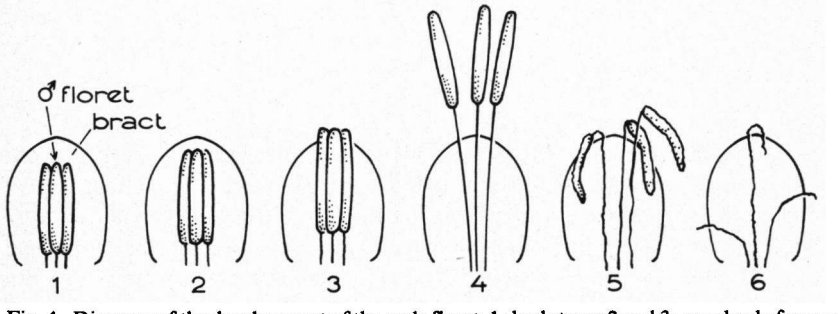

Fig. 4. Diagram of the development of the male floret. 1: bud stage; 2 and 3: one day before anthesis (3 is not found in all florets); 4: anthesis (lasts one day only); 5: post-anthesis (one day after anthesis); 6: two days after anthesis.

Anthesis lasts for one day, the 3 stamens normally developing simultaneously. In the morning before about 5 a.m. (solar time) the anthers protrude owing to a considerable elongation of the filaments. When full-grown the stamens are erect, not pendulous as in most grasses; the anthers are basifixed and non-versatile and the thecae open with a lateral, longitudinal slit. The opening of the thecae takes place between 7 and 9 a.m. when the weather is dry and not too cold, the pollen becoming shed in the course of the morning. The empty and wilted anthers drop off after a day or two; the filaments wilt the day of anthesis. Unfavourable weather conditions retard the development. When the inflorescence remains soaking wet all day, the thecae remain closed and may dehisce more or less efficaceously the next day and the filaments also wilt a day later.

4.5 The male spike

The development of the male spike is not always the same in the taxa studied. The flowering of a spike lasts for two to five days dependent on its length and on the weather. At low temperatures the flowering is protracted owing to a reduced growth so that fewer male florets attain anthesis. The uppermost male florets are often arrested in their development and reach anthesis one to three days later

than the other florets of the same spike. Anthesis does not always begin in the same part of the spike, see *fig. 5.*

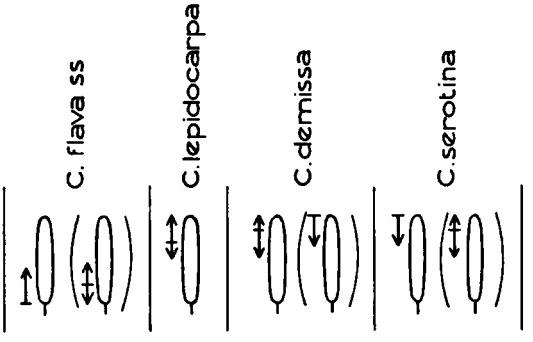

Fig. 5. Sequency of blooming in male spike.

In *Carex flava* flowering normally commences at the base of the spike but occasionally somewhere in the lower fourth of the spike (both types occurring on the same plant); in *C. lepidocarpa* it begins in the upper third of the length of the spike but never at the very tip; in *C. demissa* and in both subspecies of *C. serotina* it starts just below the retarded apical florets or (as is the rule in *C. demissa*) a little lower down.

The only exception in sequence of anthesis was observed in the *C. lepidocarpa* population L 124 from southern Belgium in which anthesis begins in the lower third of the length of the spike. In three of the plants studied for their chromosome number the meiosis was somewhat irregular but they were not sterile. In this population most of the female spikes bear male florets apically, a phenomenon frequently recorded in artificial hybrids but sometimes also found in plants belonging to true-breeding populations. The available data do not permit to conclude with certainty that population L 124 is more or less hybridogenous.

When squashes were made for meiotic divisions, it appeared that meiosis proceeds in the same way as the anthesis. The lag in development of the uppermost florets is also quite manifest. This also holds for the above mentioned population L 124.

N.B. Spikes developing after the main flowering period come into flower acropetally, so that in *C. lepidocarpa*, *C. demissa*, and *C. serotina* the late male spikes behave differently from the earlier ones developing during the main flowering period.

4.6 The whole inflorescence (see *fig. 2*)

The sequential development of the spikes follows the same pattern in all taxa studied. The uppermost female spike starts anthesis first, followed by the female spikes below it, the lowermost ones flowering latest. Depending on the distance

between the spikes the difference may be negligible or extend to three days or even longer. The apical male spike flowers one to five days after the uppermost female one. When pollination begins at once, the more distally inserted female florets may already have wilted before the male spike comes into anthesis. As a rule the male spike starts just before or simultaneously with the anthesis of the sometimes present, remote and proximal female spike.

After flowering the scape (or culm) elongates appreciably. As far as can be ascertained the sequence of emergence of the culms of a plant is also the sequence of anthesis of the culms.

In view of the fact that the male apical spike flowers later than the lateral female ones one may wonder whether the male spike is indeed retarded. The development of inflorescences with an anomalous distribution of the sexes to be discussed presently indicates that in ambisexual apical spikes the florets attain anthesis sooner than the corresponding florets of the same sex in the lateral spikes. It also appears that in ambisexual spikes the female florets develop before the male ones. It seems as if in normal inflorescences the retardation of anthesis in the male (apical) spike is attributable to the combination of protogyny and sex distribution.

4.7 Frequently observed anomalies of the inflorescence

In the *Carex flava* aggregate the sex distribution may deviate from the nominal pattern (see *fig. 2*). For the terminology of the anomalies, see KERN & REICHGELT (1954). Anomalous inflorescences occur much more frequently during protracted flowering than during the main flowering period.

Acrandry: a female spike bears at the top 1 to several male florets which attain anthesis after those of the apical male spike and shortly before or after the coaxial female florets have attained the stage of post-anthesis. When more female spikes exhibit acrandry, the male tops attain anthesis in the same sequence as the supporting female spikes. Acrandry is regularly encountered, in cultivated specimens grown under favourable conditions more often than in 'wild' plants. It is most frequent in both subspecies of *C. serotina.*

Subacrogyny and *subalterny*: male florets at the base of the female spike and intermingled with the female florets, respectively. These anomalies are of very rare occurrence; the female florets always develop before the male ones.

Male florets in female spikes appear to be quite normal and produce pollen which has the same affinity to trypan blue in lactophenol as pollen from normal male spikes so that they do not seem to have a reduced fertility.

Female spikelets in the apical male spike are often found in *C. serotina* ssp. *pulchella* but only occasionally in the other taxa. These female spikelets are not so consistently inserted as male florets in female spikes (which are nearly always found near the apex) and may be basal or subbasal (hypogyny) but also inserted in the middle (mesogyny) or subapically (acrogyny). Mesogyny is much more common, acrogyny is rare. The female spikelets in male spikes ripen before the male ones, but also before those in the lateral female spikes. Female spikelets in a male spike have a well-developed utricle and set seed normally.

The incidence of a second male spike is very rare indeed. When present, it is the uppermost lateral spike and inserted immediately below the terminal spike even if the latter is normally long-stalked (see *fig. 2*). The second male spike flowers later but before the male flowers that may occur in the female spikes.

When more than two female spikes occur in the upper region of the inflorescence the second from the top may be precocious. In such cases the uppermost female spike is inserted immediately below the male spike and much smaller than the one below it.

Branched female spikes originate when instead of a single spikelet bearing a single floret a spike of the second order develops in the axil of a scaly bract. That this anomaly is a lateral spike and not a spikelet with several florets is quite clear from the fact that each floret has its individual utricle (see p. 6). At its base the spike axis of the second order is surrounded by a utricle which often contains a functional or sterile female floret, and at its apex it may bear one to a few male florets each subtended by a bract. Such lateral spikes of the second order are only found in the axils of the lowermost bracts of the lowermost first order spike or spikes; they occur in all five taxa studied and have also been recorded in the section *Acutae* of *Carex* by FAULKNER (1970), as a rule in well-developed inflorescences especially in lush, cultivated specimens. The second order spikes develop later than their motherspikes do.

In cultivated *C. serotina* ssp. *pulchella* terminal male spikes with numerous, lateral female spikelets are found regularly. The sequence of maturation of the remaining male florets is often disturbed in such inflorescences and usually begins near the group of female spikelets instead of basipetally from near the apex.

The occurrence of apically inserted male florets in female spikes may well have adaptive significance: since they come into flower after the apical male spike, they stretch the period during which pollen is shed and increase the chances of successful pollination. This is especially important during the protracted flowering because in the relatively small number of inflorescences not every day a male spike produces pollen. In *C. serotina* the incidence of androgyny in female spikes may also be an adaptation against rabbit damage: especially in populations of the ssp. *pulchella* the apical portions of the inflorescences had often been bitten off before the male spike had flowered.

5. FLOWERING IN HYBRIDS

The above mentioned flowering patterns are those of inflorescences producing viable seeds. Artificial and natural, wholly or partly sterile plants sometimes deviate from these patterns. Since a more detailed discussion will be published later, only a few characteristics indicating their hybrid nature will be mentioned here:

- The male and/or female florets do not attain anthesis but remain undeveloped in the bud stage.
- Female florets develop in an apparently normal way, but do not set seed.

– The stamens are not a bright yellow but greyish-yellow. They protrude more slowly and/or later during the day and dehisce late or incompletely; when wilted they persist longer on the spike.
– The stigmas are smaller.
– The female spikes all bear large numbers of male florets.

6. COMPARISON OF THE FLOWERING PERIODS

6.1 Principal flowering period

This comparison will be based on the male anthesis only. Because each male floret is in anthesis during a single day and there is normally only a single male spike, while a female floret stays in anthesis for several days and there are a number of female spikes per inflorescence, the total period of male anthesis does not last so long as the total period of female anthesis. That is why the male anthesis discriminates more sharply in a comparative study of flowering periods than does the female anthesis. The length of female anthesis varies with the rate of pollination and with the number and the place of insertion of the female spikes. It is, therefore, no reliable basis of comparison.

Generally speaking the sequence of flowering is as follows: *C. lepidocarpa*, *C. demissa*, *C. flava*, *C. serotina* ssp. *serotina*, and *C. serotina* ssp. *pulchella*. This sequence was also found in specimens transplanted from their natural habitat in the experimental garden. Within each taxon there is an apprecial range of flowering, however, so that, for instance, late flowering *C. demissa* populations may come into anthesis simultaneously with, or even later than the earliest

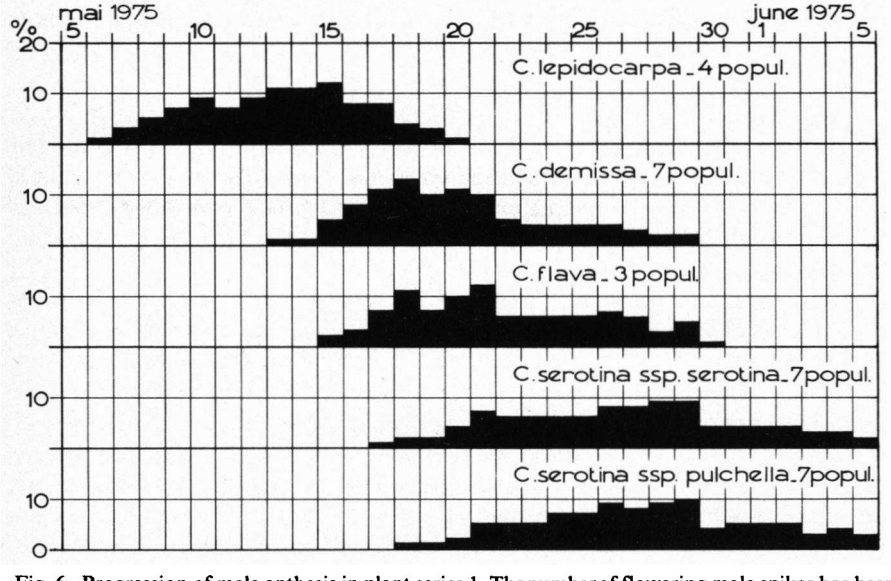

Fig. 6. Progression of male anthesis in plant series 1. The number of flowering male spikes has been indicated in per cents. of the sum of the daily counts per taxon.

flowering *C. serotina* population. However, when two or more taxa occur sympatrically in a small area, their sequence of anthesis is always consistent.

The counts of series 2 and 3 yield comparable results. The counts are not statistically warranted random samples because the recorded data are not all mutually independent: a male spike may flower for several consecutive days, and in plants with several inflorescences the sequence of flowering is not at random. The first dates of flowering per plant are independent records, however. By means of a statistical test according to Kruskal & Wallis (see DE JONGE 1963) it was attempted to estimate per population in how far these initial flowering dates differ significantly (see *fig. 7*). Since in a number of population samples there are non-flowering specimens (see *table 1*), the samples need not be quite representative in a statistical sense, so that the results of the test can only be used to obtain an overall impression of the differences among the numerous samples.

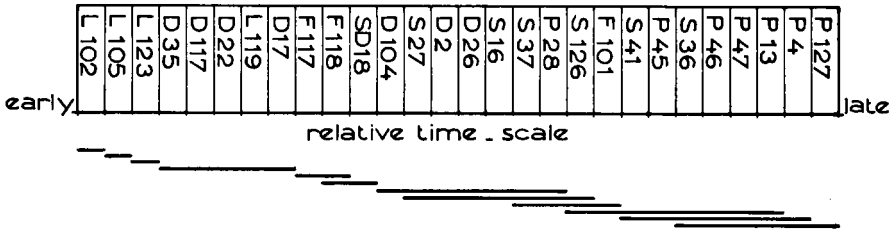

Fig. 7. Differences between population samples in the initiation of male anthesis.
The commonly underlined population-samples differ not significantly in the initiation of male anthesis.

It appeared that there is no correlation between flowering time and geographical latitude. Although the Swedish populations of *C. lepidocarpa* flower last, the German ones of *C. flava* flower later than the Scandinavian ones; moreover, the distribution of the start of the flowering period of the *C. demissa* populations shown in *fig. 7* has no relation with the area of origin.

A difference in flowering time of only a few days may nevertheless be very important because when two related *Carex* taxa occur sympatrically, the one flowering later will run a greater chance of producing hybrids than the one flowering earlier, because owing to their protogyny, the female flowers of the taxon flowering later will sooner receive pollen of the earlier one than pollen of its own species. Conversely, the taxon flowering earlier will initially only receive legitimate pollen, so that most female florets will have been pollinated before nonspecific pollen is available. Assuming that some certation occurs when illegitimate pollen tubes start growing, the incidence of hybridisation may be reduced, but the effect of the protogyny on the chances of hybrid offspring may prevail. In principle the taxon flowering later may have a somewhat reduced change of

survival on account of its partially hybridogenous (and in this case usually partly sterile) offspring. The replacement of one species by another, related one is of course largely dependent on their respective ecological requirements (which may be the decisive competitive factor), so that the effect of the difference in flowering time on selection and survival cannot so easily be studied in natural populations.

Table 1. Fertility and protracted flowering in plant series 1.

population	country	number of plants					rate of protracted flowering at 22 June
		total	fertile	(partly) sterile	vege-tative	dead	
L 102	G	54	40	0	12	2	–
L 105	G	54	22	0	31	1	–
L 123	B	54	40	0	11	3	–
D 35	N	36	28	0	3	5	–
D 117	S	39	28	0	8	3	–
D 22	N	54	49	0	5	0	+
L 119	S	36	22	0	14	0	–
D 17	N	54	47	0	7	0	+
F 117	S	69	52	2	8	7	–
F 118	S	54	28	16	9	1	–
SD 18	N	54	37	5	5	7	+
D 104	G	54	32	0	17	5	–
S 27	N	54	46	4	0	4	+++
D 2	N	36	27	0	7	2	+
D 26	N	36	33	0	3	0	+
S 16	N	54	36	5	9	6	+++
S 37	N	54	44	1	8	1	++
P 28	N	42	39	0	1	2	+++
S 126	G	36	30	1	4	1	+++
F 101	G	54	39	0	12	3	–
S 41	N	54	41	1	8	4	+++
P 45	N	54	49	0	3	2	+++
S 36	N	54	35	0	15	4	++
P 46	N	54	36	3	9	6	+++
P 47	N	36	20	0	10	6	+++
P 13	N	54	22	0	25	7	+++
P 4	N	54	43	0	5	6	+++
P 127	N	36	24	0	7	5	+++

Countries: N = Netherlands; G = West-Germany; B = Belgium; S = Sweden.
Rate of protracted flowering: – = no protracted flowering; + = less than 1/4 of specimens is flowering; ++ = 1/4 to 1/2 of specimens is flowering; +++ = more than 1/2 of specimens is flowering.

6.2 Protracted flowering

Various aspects of the protracted flowering have already been mentioned. From observations of all cultivated plants it can be deduced that in all studied populations of *C. serotina* protracted flowering occurs till the end of August or even the middle of September. Many populations of *C. demissa* exhibit protracted anthesis in June and July, whereas the other two species never showed any true protracted flowering, but may occasionally produce a new inflorence shortly after their main flowering period. As far as can be ascertained natural populations behave in exactly the same way. Protracted flowering was more frequent in *C. demissa* according as the main flowering was poorer. It is known that specimens of populations of other plant species subjected to mowing show protracted flowering when mowed off early (see, e.g., LONDO 1977). The number of late inflorescences is always appreciably lower than that developed duringthe main flowering period. In *C. serotina* most adult specimens exhibit a much protracted anthesis in nature, but the late inflorescences are more numerous at sites inundated during the cold season and in such localities the main flowering period may be altogether suppressed. The biological significance of protracted flowering in *C. demissa* is that it occurs as a compensation of a low rate of flowering during the principal flowering period, whereas in *C. serotina* it is of regular occurrence and represents an important portion of the total production of seeds.

The phenomenon under discussion may also have something to do with the capacity of flowering during the first growing season. In the series 3 of cultivated plants only *C. serotina* (both subspecies) came into flower in the first year of growth. The 18 plants of ssp. *pulchella* produced from 3 to 14 inflorescences (mean 9, s.d. 2.6). The 46 plants of ssp. *serotina* produced from 0 to 15 inflorescences (mean 6, s.d. 3.9). Among all other cultivated specimens also only *C. serotina* came into flower during the first season, provided the seeds had germinated before the end of May. Flowering starts in the second half of July and lasts till the middle of September.

7. THE RELATION BETWEEN THE TEMPERATURE AND THE RATE OF DEVELOPMENT OF THE INFLORESCENCE

The development of the inflorescences, like all growth processes, is dependent on the prevailing temperature. This explains why the duration of a certain flowering phase and the time-lag between two flowering stages may vary considerably (see p.6–9).This dependence on the temperature also holds for the number of male spikes attaining anthesis simultaneously: since the male florets only open during early morning the number of male spikes in anthesis is largely determined by the temperature of the preceding day. This means that the effect of the temperature is only visible one day later, which is evident from a comparison between the number of male spikes in anthesis after days with low temperatures and after days with high temperatures, as shown in *fig. 8*.

Since the growth rate is temperature-dependent, and varies with the prevailing

weather conditions, it is not constant in time. The abscissa in the *figs. 6* and *8* is a metric time-scale, but an ordinal scale for the growth. (In an ordinal scale only the sequence is meaningful and not the length of the intervals.) That is why it was necessary to choose a distribution-free test for the comparison of the commencement of male anthesis based on sequential numbers (see p. 12).

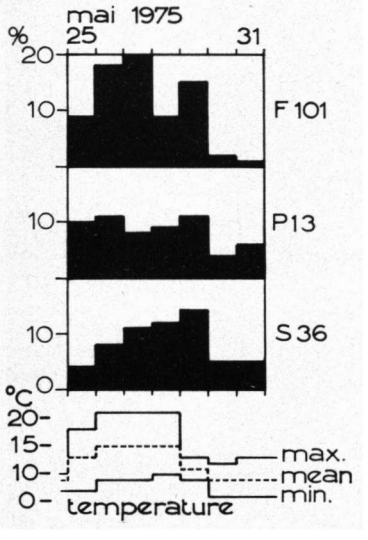

Fig. 8. Effect of the temperature on the relative incidence of male flowering. The number of flowering male spikes is given in percentages of the sum of the daily counts per population sample.

8. THE MODE OF REPRODUCTION

The floral morphology points to an anemophilous pollination: there are no attractive semaphylls, no nectar is produced, the stamens are long-exerted, and the stigmas are covered by a great many patent papillae. Direct observations in the experimental garden agree with this supposition. Gusts of wind blow away small clouds of pollen. Pollen-gathering insects were never observed, not even during the early morning when the anthers still contain most of their pollen and insects (such as certain hover flies) are visiting, e.g., *Plantago lanceolata* growing near the *Carex* plots. Fruit setting is copious, so that one may conclude that the anemogamy is very effective.

Incidental observations of natural populations did not yield indications of entomophily either (for instance insect damage to anthers was never noticed). Although visiting by insects cannot be excluded altogether (pollen of *Cyperaceae* is frequently found in the guts of certain syrphids: Leereveld and Stelleman, unpublished), the evidence clearly points to the prevalence of anemophily in the five taxa studied.

Plants raised from seed of the populations F 101, L 102, L 105, D 2, D 22, D 24, S 27, P 5 and P 6 in the experimental garden were transplanted in private gardens in such a way that only selfing could take place. The seeds produced by such

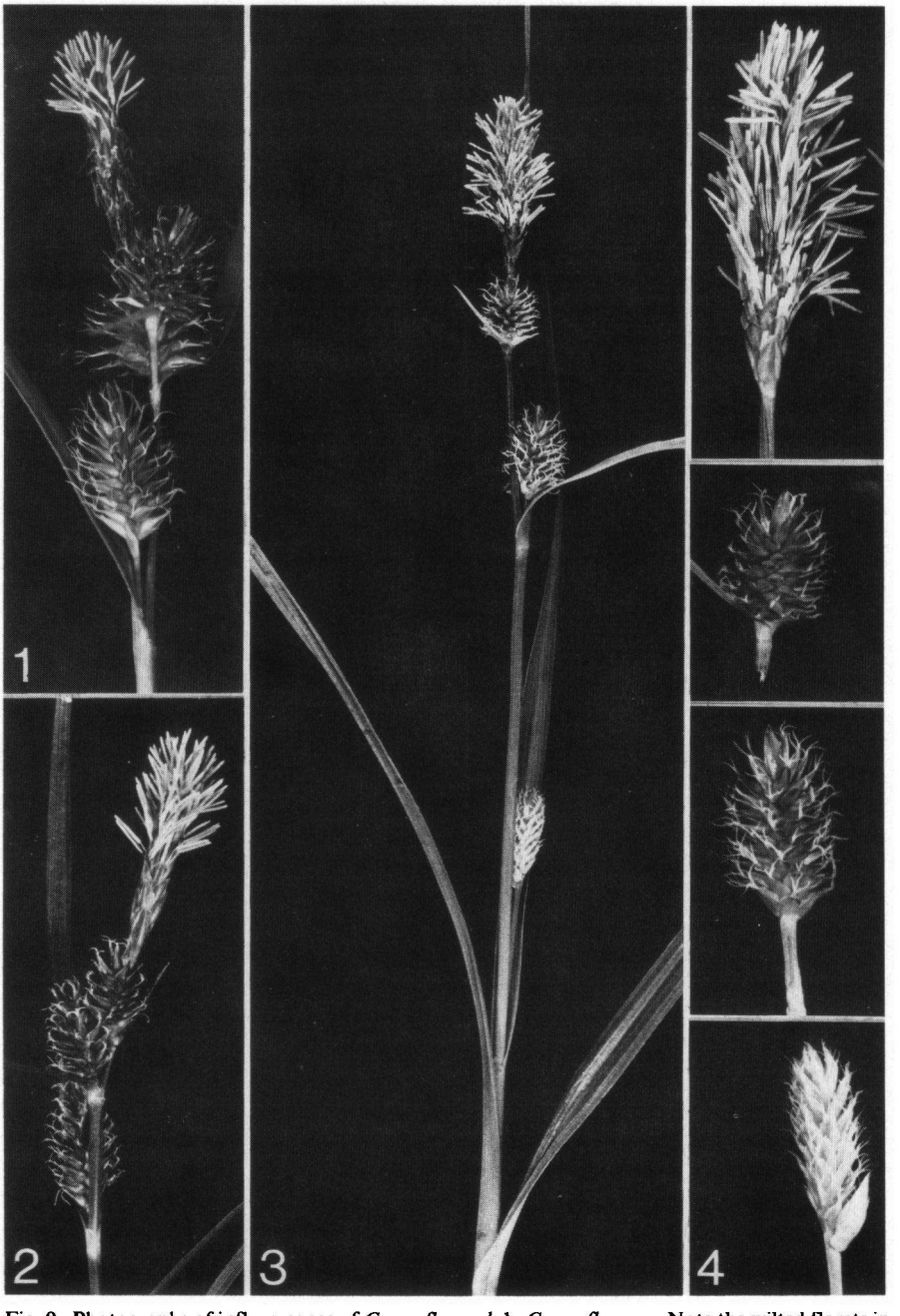

Fig. 9. Photographs of inflorescence of *Carex flava s.l.* 1: *Carex flava s.s.* Note the wilted florets in the lower part of the male spike.
2: *Carex demissa.* Note the florets in bud stage in the lower part of the male spike.
3: *Carex demissa.* An inflorescence with a remote female spike.
4: Details of the spikes in photo 3. Note the differences in development between the female spikes, the male flower in bud stage at the top of the second female spike, and the spike of the second order at the base of the lowermost female spike.

plants were sown in the experimental garden and proved to be viable. Hybridisation experiments to be published later showed that outbreeding yields normal seed (and that even crosses between different species can easily be made). Also the incidence of sterile plants (most probable of hybrid origin) in natural populations points to at least some allogamous pollination under natural conditions. The relative importance of autogamy and allogamy has not been studied.

9. DISCUSSION

It is noteworthy that in all taxa studied, *C. flava* excepted, during the main flowering period male anthesis does not proceed acropetally as is normal in a spicate inflorescence, but basipetally. BARNARD (1957), SCHULTZE-MOTEL (1959) and SMITH (1966) who all studied the development of *Carex* inflorescences anatomically, did not mention an anomalous progression of the development in the male spike. According to SMITH (1966) the inflorescences flowering in spring are already formed during the previous growing season and remain dormant during the cold season. Conceivably the inflorescences produced during protracted flowering originate during the spring and early summer and develop immediately without a period of dormancy. This must at any rate be the case in those specimens of *C. serotina* already flowering during their first growing season. One must also bear in mind that male florets of late inflorescences attain anthesis acropetally, so that there may be some relation between the sequence of male flowering and dormancy, but if this is in case, the flowering sequence in the male spike of *C. flava* remains unexplained. There are no references to these points in the pertaining literature.

There is some discrepancy as regards the position of the stamens of *Carex* when producing pollen. KUGLER (1970) and JERMY & TUTIN (1968) report pendulous stamens. On photographs and in some drawings (see, e.g., PROCTOR & YEO 1973 and WETTSTEIN 1935) they appear to be patent to erect; in KEBLE-MARTIN (1965) they are sometimes drawn as patent and sometimes as drooping. In all five taxa studied by the present author they are patent to erect. Only empty, wilting stamens and stamens loaded with water drops in wet weather may droop. Reports and drawings suggesting pendulous filaments in *Carex* obviously refer to observations of wet or wilted material (or of herbarium specimens in which the filaments became limp before or after drying!).

Preliminary observations suggest that during the main flowering period there may be more than one peak in the frequency diagram. This may explain the prolonged or repeated flowering in *C. demissa* and *C. serotina* as a mutual and separating shift of these peaks. However, the effect of the temperature on the quantitative rate of flowering (see p. 14) is such that in the circumstances of an experimental garden it is impossible to establish whether the frequency diagram has more than one maximum. There is an argument against the supposition that the protracted flowering is merely a 'postponed' part of the main flowering period, however. As mentioned before, the inflorescence primordia of the main

flowering phase are already formed during the preceding growth season whereas those of the late ones originate in the year of flowering. The induction mechanism of the phenomenon of protracted or renewed flowering would in this case not be a prolongation of an existing inductive period, but a separate one attributable to the annihilation of the normal flowering induction during the late summer and autumn.

Data gleaned from the pertaining literature show that the records of the flowering periods of the *C. flava* complex vary a great deal.

HEUKELS – VAN OOSTSTROOM (1970) mention for *C. flava* and *C. lepidocarpa* May and June, for *C. demissa* June and July, for *C. serotina* May till September; CLAPHAM et al. (1962) mention for *C. lepidocarpa* May and June, for *C. flava* and *C. demissa* June, for *C. serotina* May till August; ROTHMALER (1970) mentions for *C. lepidocarpa* and *C. flava* June and July, for *C. demissa* May till July, for *C. serotina* ssp. *serotina* May till September, for *C. serotina* ssp. *pulchella* June till August; DAVIES (1953) mentions for *C. lepidocarpa* May and June, for *C. scandinavica* (which is most probably synonymous with *C. serotina* ssp. *pulchella)* May till July and for *C. serotina* 'at least a month later than the other species'.

The fact, that floras mention varying flowering periods may be explicable by local climatologic differences, but it may also indicate that the observations are inaccurate. The small differences in flowering periods, as mentioned in the present study, will be hardly detectable by occasional observations of isolated natural populations. The varying sequences of the start of the flowering of the species in the different floras are at variance with the records of the present author. Only for *C. serotina* there may be great differences as consequence of inundation of the growing site. The deviations of the sequence *C. lepidocarpa* – *C. demissa* – *C. flava* – *C. serotina* ssp. *serotina* – *C. serotina* ssp. *pulchella* are not consistent, what may be another indication of the inaccuracy of the records in the floras. A number of authors mentioned June as the beginning of flowering of one or more of the species of the *C. flava* – complex, whereas others, like the present author, report May. A possible explanation is that most species of *Carex* in the phase of anthesis cannot be satisfactorily named so that, as a rule, only specimens with well developed utricles end their life in a herbarium, and the recorded collecting dates tend to be on the late side. The extended flowering period of *C. demissa* and *C. serotina* is generally known, but nobody points out its ecological significance.

The comparison of the four species investigated: *Carex flava, C. lepidocarpa, C. demissa, C. serotina* reveals that the latter species deviates from the other three in various respects, viz., a) *C. serotina* is the latest to come into flower,

b) *C. serotina* is the only one flowering already in the first growing season,

c) *C. serotina* has an extended flowering period responsible for an appreciable portion of the total seed crop (although *C. demissa* exhibits the same characteristic, there is a marked quantitive difference), and

d) androgyny of the spikes is of far more frequent occurrence in *C. serotina* than in the other species.

These differences are to be explained as an adaptation to the specific habitat of *C. serotina*, edges of fens and lakes and dune valleys with a variable water level. In both habitats the water table may vary from year to year at one site, so that it is of importance that the plants already produce seed during their first year, because it is not certain whether they may survive to start a subsequent growing season. Besides, in the habitat in question damage by rabbits is much more frequent than in the preferred habitats of the other species, so that one may interpret the capacity to produce inflorescences throughout the growing season as an adaptation to grazing.

10. CONCLUSIONS

The three questions posed in the introduction can be answered as follows:
1. The only difference in the mode of flowering is in the development of the male spike wich proceeds acropetally in *C. flava* but starting from or just below the top, basipetally in the other taxa.
2. The flowering periods differ somewhat so that there is a sequence *C. lepidocarpa* – *C. demissa* – *C. flava* – *C. serotina* ssp. *serotina* – *C. serotina* ssp. *pulchella*, but there is a considerable overlap. There are greater differences in the degree of second or extended flowering.
3. All species are protogynous and strictly anemophilous. They produce viable seeds both autogamously and allogamously.

These results demonstrate quite clearly that the mode of flowering does not constitute any barrier preventing hybridisation within the *C. flava* complex, which conclusion is confirmed by the fact that hybrids were raised from seeds collected in natural populations.

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