

A STUDY OF THE FLOWERING PHENOLOGY OF *TARAXACUM* MICROSPECIES IN SOME BIOTOPES IN THE NETHERLANDS AS OBSERVED DURING THREE SUCCESSIVE YEARS

A. A. STERK and M. M. LUTEIJN

Vakgroep Bijzondere Plantkunde, Universiteit van Amsterdam, Plantage Middenlaan 2a, 1018 DD Amsterdam

SUMMARY

During three consecutive years (1980–1982) the flowering pattern of dandelion populations has been studied in five habitats. The time course of the main (spring) flowering period may vary in different years per plant and per population, partly due to differences in microclimate, but there are also genetically controlled differences between microspecies in the attainment of maximum spring flowering. In addition there may be appreciable differences in the late-flowering pattern, both between populations and individual plants. Per site, the seasonal periodicity may vary in different years. Apart from 'normal' years, there are also dandelion-rich and dandelion-poor years. The amount of sunshine in the spring is presumably partly responsible for such differences.

1. INTRODUCTION

Flowering of dandelions is a striking phenomenon in The Netherlands and emphasises the fact that *Taraxacum* belongs to the most common elements of the Dutch flora.

The genus is represented by 6 sections (HAGENDIJK et al. 1975, 1982; ØLLGAARD 1983). Sect. *Obliqua* is restricted in its distribution to the coastal zone, sect. *Erythrosperma* occurs both along the coast and inland chiefly in open grassland types on dry and humic sandy soils, the rare sections *Palustria* and *Spectabilia* are restricted to little manured or grazed grasslands, and the sections *Hamata* and *Taraxacum* (= *Vulgaria*, by far the largest) are very common and wide-spread. The last two are usually found at trodden sites and in lawns, road sides and fertilized and grazed pastures. Especially in the heavily fertilized, and cattle-grazed grassland of the *Poo-Lolietum* type (WESTHOFF & DEN HELD 1975) their population densities may attain very high values, which results in an intense yellowing of the pastures. It is striking that the degree of yellowing is often different in two adjacent lots, which is highly suggestive of an appreciable influence of the local agricultural regime upon the population densities and the opulence of flowering of *Taraxacum*. It has been shown that the various kinds of ecologically different agricultural pastures support a different *Taraxacum* flora (STERK

et al. 1983).

There are only very few data available concerning the flowering phenology of *Taraxacum* in different biotopes in The Netherlands (HAGENDIJK et al. 1975, 1982; LOENHOUD & VAN DER HEIJDEN 1980; STERK 1982; LONDO 1977, 1983). An adequate insight into the quantitative aspects of the flower and seed production is required for an understanding of the reproductive strategy of the dandelions, the more so since recently also diploid and sexual biotypes have been recorded from The Netherlands. There are some indications that these diploid biotypes only come to bloom in the springtime and not later in the year, whereas agamospermous ones may also flower later, in the summer and/or the autumn (STERK et al. 1982). This may have a considerable bearing upon the population biology of these different biotypes. The present study concerns the results of field studies of the periodicity of flowering and the production of capitula of agamospermous triploids of the sections *Hamata* and *Taraxacum* carried out during three successive years (1980–1982) in five biotopes.

In order to get some insight in the genetical differences in flowering phenology between microspecies of sections from disturbed habitats (sect. *Hamata* and *Taraxacum*) and from relatively undisturbed ones (sect. *Palustria* and *Spectabilia*) the flowering of some representatives of these sections has been studied under uniform conditions in the experimental garden.

Elsewhere in Europe and in the U.S.A. the flowering of *Taraxacum* has been recorded by PERCIVAL (1955), FÜRNKRANZ (1960), HOFSTEN (1954), LISTOWSKI & JACKOWSKA (1965), SOLBRIG (1971) and GRAY et al. (1973). Many reports deal with the competition between dandelions and fruit crops in relation to bee pollination (FILMER 1941, FREE 1968).

2. METHOD, SITES OF RECORDING AND TAXA STUDIED

The present investigation was carried out from 1980–1982 in five very diverse biotopes in the area of Abcoude (Prov. of Utrecht). In *table 1* the most relevant ecological data regarding the biotopes have been summarized. The situation of the localities is as follows:

Site 1: North-facing ramp of motorway A9 between Abcoude and Amstelveen (= 'North ramp').

Site 2: South-facing ramp of the same way (= 'South ramp').

Site 3: Highest part of road bank near the viaduct of the motorway near the turn-off for Abcoude coming from Amsterdam (= 'Viaduct bank').

Site 4: Lawn in the municipality of Abcoude, near the Town Hall (= 'Lawn').

Site 5: Pasture in municipality of Abcoude facing the freeway near turn-off Abcoude coming from Utrecht (= 'Pasture').

Weekly at each site the number of flowering dandelions was counted within a fixed and marked sampling plot. At site 2 of 10 individually marked plants also the number of flowering heads was recorded in 1981 and 1982.

In order to distinguish between the effect of environmental differences and that of genetical ones, 25 plants, each from the North- and South ramps, the Lawn and the Pasture were grown under uniform conditions in the experimental garden in Amsterdam. The plants were dug up and potted in a fertile garden soil mixture in August 1981. In 1982 the rate of flowering was recorded by counting the number of capitula produced. In the same year, like-wise under uniform conditions, the flowering phenology of 9 microspecies of *Taraxacum* sown in July 1981, was studied.

The specific composition of the dandelion-flora of the biotopes studied is shown in table 1. For the nomenclature, HAGENDIJK et al. (1982) and OLLGAARD (1983) are followed, for those of the other taxa HEUKELS-VAN OOSTSTROOM (1977).

Table 1. Survey of ecological data regarding the biotopes and representation of microspecies of (1) sect. *Hamata* and (2) sect. *Taraxacum*.

Locality	1	2	3	4	5
Use	Bank	Bank	Bank	Lawn	Pasture
Size of sample plot	100 m ²	150 m ²	100 m ²	150 m ²	100 m ²
Exposure	N	S	—	—	—
Slant	c. 30°	c. 30°	—	—	—
manuring	none	none	none	little	heavily
Grazing	none	none	none	none	intensive (cattle)
Mowing	twice yearly	twice yearly	twice yearly	once every ten days	a few times per year
Soil	humic sand on sand	humic sand on sand	humic sand on sand	sandy clay	clay
<i>T. alatum</i> (2)		+			+
<i>T. ancistrolobum</i> (2)			+	+	+
<i>T. atonolobum</i> (2)			+		
<i>T. atrovirens</i> (1)	+				
<i>T. aurosulum</i> (2)					+
<i>T. calochroum</i> (2)	+				
<i>T. croceiflorum</i> (2)					+
<i>T. effusum</i> (2)			+		
<i>T. ekmanii</i> (2)		+	+	+	+
<i>T. eudontum</i> (2)	+	+	+	+	
<i>T. fagerstroemii</i> (2)	+		+	+	
<i>T. falciferum</i> (2)		+			
<i>T. hamatulum</i> (1)	+		+	+	+
<i>T. maculatum</i> (2)		+			
<i>T. olitorium</i> (2)		+			
<i>T. sellandii</i> (2)	+	+	+	+	+
<i>Agrostis stolonifera</i>	+			+	+
<i>Dactylis glomerata</i>	+		+	+	+
<i>Elytrigia repens</i>	+	+	+		+
<i>Festuca rubra</i>	+	+	+		+
<i>Glyceria maxima</i>					+

Table 1 (continued)

	(1)	(2)	(3)	(4)	(5)
<i>Holcus lanatus</i>	+	+			+
<i>Lolium perenne</i>	+	+		+	+
<i>Phleum pratense</i>					+
<i>Poa annua</i>				+	+
<i>Poa pratensis</i>	+	+	+	+	
<i>Poa trivialis</i>				+	+
<i>Achillea millefolium</i>			+		
<i>Anthriscus sylvestris</i>			+		
<i>Bellis perennis</i>				+	+
<i>Capsella bursa-pastoris</i>		+		+	
<i>Cardamine hirsuta</i>	+	+	+	+	+
<i>Cerastium fontanum</i>	+			+	+
<i>Cirsium vulgare</i>	+	+			
<i>Erophila verna</i>		+			
<i>Ficaria verna</i>				+	+
<i>Galium aparine</i>			+		
<i>Geranium molle</i>		+	+		
<i>Glechoma hederacea</i>		+	+		
<i>Heracleum sphondylium</i>			+		
<i>Hypochaeris radicata</i>	+				
<i>Lamium purpureum</i>		+			
<i>Matricaria maritima</i>		+			
<i>Plantago lanceolata</i>	+	+			
<i>Ranunculus repens</i>	+		+		+
<i>Rumex acetosa</i>	+		+		+
<i>Rumex crispus</i>		+			
<i>Rumex obtusifolius</i>		+			
<i>Senecio vulgaris</i>	+	+			
<i>Stellaria media</i>	+	+	+		+
<i>Trifolium repens</i>				+	+
<i>Urtica urens</i>				+	
<i>Veronica chamaedrys</i>		+		+	

3. RESULTS

3.1. Populations

3.1.1. The principal flowering period in the different biotopes and in the different years

Fig. 1 shows the main flowering period of the dandelion populations in three consecutive years. This main period appears to fall in the months of (March) April and May and proceeds upon the whole in the same way in all biotopes studied, usually showing more or less normal distribution. It is clear that in the different biotopes the flowering is not simultaneous but shows a shift, which was most manifest in the diagrams of 1980. The flowering starts in the South ramp and also attains its peak sooner, to be followed by, successively, the Via-

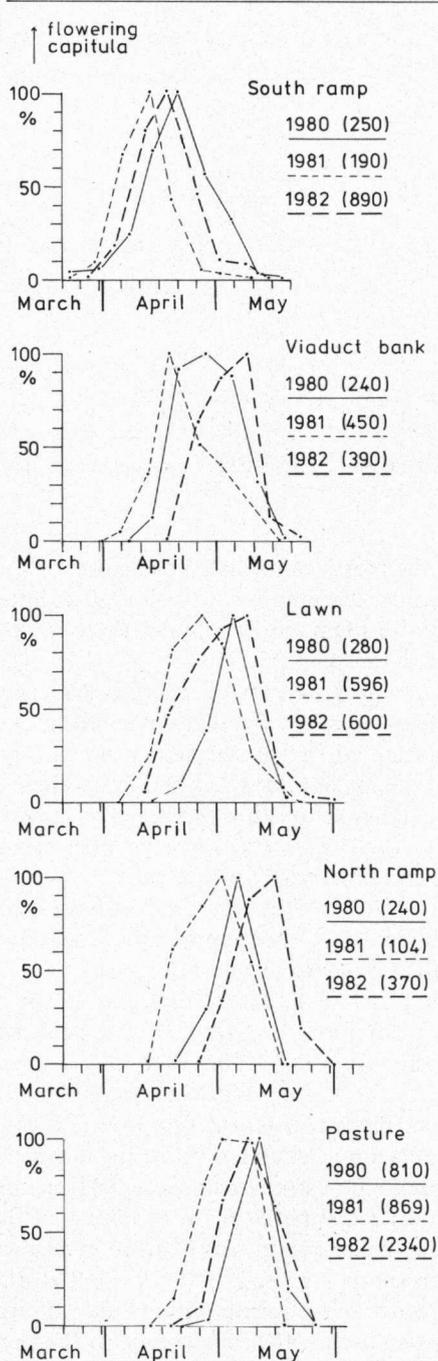


Fig. 1. The principal flowering period of *Taraxacum* in 5 biotopes during 3 successive years. Flowering expressed as percentage of the flowering capitula.

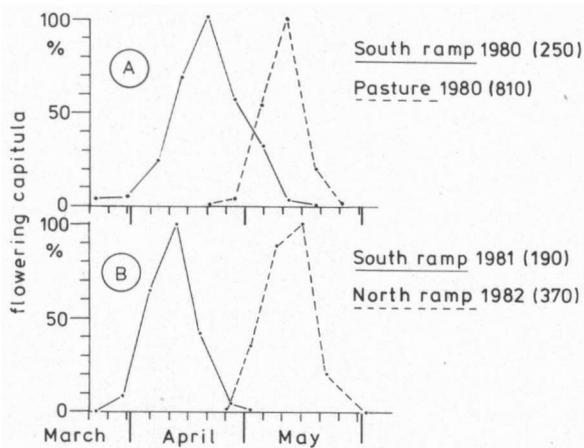


Fig. 2. Principal flowering periods of 2 populations expressing the greatest differences in the same year (A) and in different years (B).

duct bank, the Lawn, the North ramp and the Pasture.

Fig. 2A shows the most extreme records of 1980 together, which indicates that the height of the flowering period is attained three weeks later in the Pasture than it does on the South ramp.

Although no actual records were made, there is evidence that this sequence is largely caused by temperature differences. The critical temperature for the onset of flowering is attained first in the spring on the sandy and S-exposed South ramp, and also the maximum is reached first. The last site to come into flower is the low-lying and moist pasture where the soil temperature starts rising relatively late and only slowly. The other three biotopes occupying an intermediate position in the sequence recorded for that year.

Fig. 2B shows the extremes in the course of flowering recorded in the present study. Clearly the principal period of flowering in the diverse biotopes and in different years may fall at times up to a month apart.

As might be expected there is manifest difference in the course of flowering in the same biotope in different years (fig. 1). The peak was attained earliest at the South ramp in the years 1981–1982–1980 in this sequence, and the same was noted at the Pasture and less obviously so on the Lawn. The sequence was different at the Viaduct bank and North ramp, viz., 1981, 1980, 1982. When the course of the temperature, calculated as the mean per decade at 2 m above ground level at Schiphol (the closest meteorological recording station during the years of observation) is compared with the course of flowering, it appears that the sequence of the mean rise in temperature agrees with the sequence in flowering at the South ramp site, viz., 1981–1982–1980. It seems permissible to accept that the sequence of flowering onset is indeed largely attributable to a temperature effect. Also in the other environments the flowering commenced earliest in 1981, but in 1980 and 1982 the sequence was reversed. Possible causes

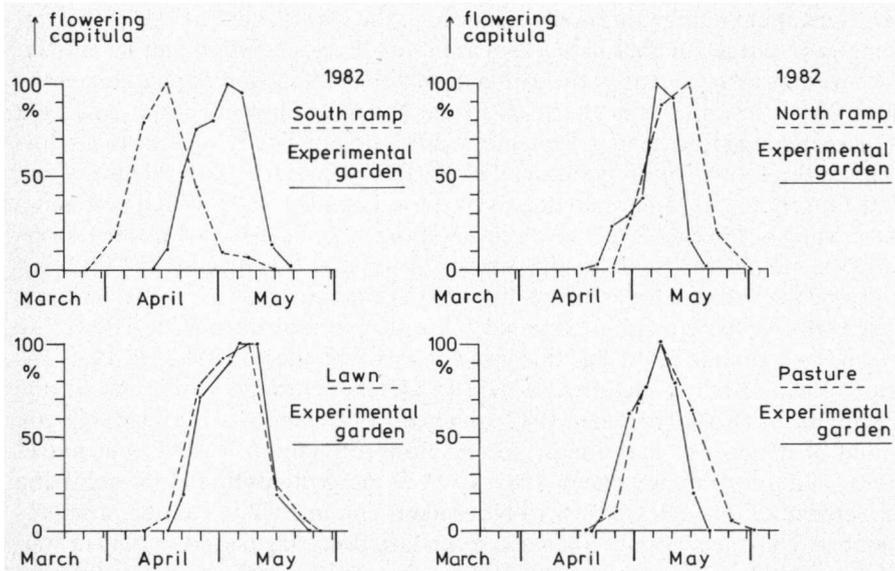


Fig. 3. Principal flowering in nature and in the experimental garden. The population-samples have grown up under the same conditions.

of the relatively late commencement of regrowth and of flowering in 1982 are the accumulation on the flat Viaduct bank of salt applied against snow and iced roads, and the presence of late snow on the North ramp.

3.1.2. The principal flowering period under uniform conditions

In the previous paragraph the conclusion was drawn that in the different biotopes the difference in the main flowering periods is mainly to be ascribed to environmental factors. However, such differences might also be attributable to genetical differences, since at the different sites not the same assemblies of microspecies are present and different microspecies (or different populations of a single microspecies) are likely to exhibit genetically controlled differences. In order to elucidate this point 25 individual plants from each site studied were grown under uniform conditions and compared as to their flowering behaviour with that at the original localities (see *fig. 3*). It appears that the differences recorded in the field disappear when dandelion plants are transplanted into an experimental garden. These observations confirm the above-mentioned supposition that the differences in the manner of blooming observed in the field are principally the result of environmental factors (in particular temperature effects).

3.1.3. Seasonal periodicity of flowering

The seasonal flowering periodicity at the five sites is shown in *fig. 4*. On the ordinate axis the time and on the other one the percentage of capitula is plotted.

The maximum number of heads produced in the spring is put at 100%; the percentages recorded in the summer and autumn are calculated on that maximum. The records show that after the spring flush not all dandelion populations come into flower again later in the year. In the North ramp population, barring a single specimen flowering in September, 1982, no late flowering was noted during the three years of observation. The Pasture population showed hardly any late flowering: only a few individuals on a total number of, at a rough estimate, something like over 6000 plants. A clearly more complicated post-spring flowering was seen at the South ramp, Viaduct bank and Lawn sites. The different rate and the different times of late flowering in different years are rather striking. The South ramp population exhibited a clear-cut, concentrated second flowering period in 1980 and 1981, but this was not at all manifest in 1982. In 1980 this second period fell in October, in 1981 in October through November till the beginning of December and in 1982 principally in November. The Viaduct bank stand of dandelions had a clear second flowering period in 1980, but not in 1981, and a very minor one in 1982. In 1980 the post-spring bloom occurring in September through October to November, and in 1982 in October and November. The Lawn population had a secondary flowering period in 1980 in September-October-November, one in 1981 in September-October and in 1982 one in August.

The mode of flowering outside the main blooming period is a varied one. In cases of a clearly marked second period this usually falls in September to November, extends over a longer stretch of time and has not such a pronounced maximum as the spring flowering. Especially in the Lawn a relatively large number of heads is consistently present throughout the growing season or even all the year round, also in high summer especially also in August.

Table 2 shows these phenological records, the total number of capitula counted per biotope and per year being used as the starting point and put at 100%. It follows from this table that usually during the principal (spring) flowering period the highest score of the whole year is recorded, but sometimes the total number of heads produced during post-spring blooming may exceed that formed in the spring. This is the case at the South ramp in 1981 and on the Lawn in 1980. At the Lawn site about 30% of the heads were produced outside the main flowering period in 1981 and 1982. In the table the percentages of capitula produced late in the year are divided in those recorded during the months 9-10 and those found in 11 and 12. This was done because experience has taught us that most of the achenes formed during November/December, in contrast to those produced in September/October, are abortive, so that the 'late' heads do not contribute towards the reproduction of the population; the same holds for achenes produced in January/February.

The possible causes of the yearly differences in seasonal periodicity have hardly been investigated. The differences may be attributable to environmental causes and/or the genetical make-up of the taxa present (compare 3.1.2).

As regards environmental effects, there are appreciable ecological differences between the various biotopes and in each biotope in turn differences may occur

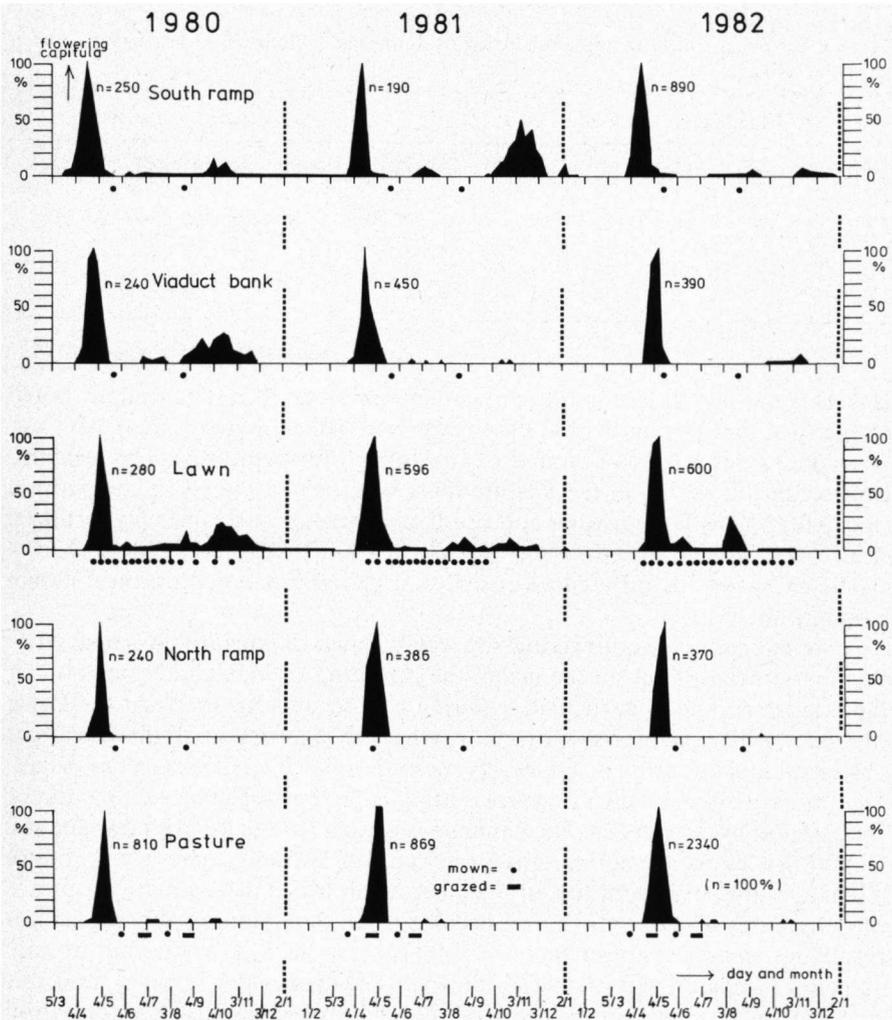


Fig. 4. Seasonal periodicity of flowering of *Taraxacum* in 5 biotopes in 3 successive years. Maximum number of flowering capitula counted in the spring put at 100%.

in consecutive years. The difference between the North and South ramps is rather spectacular and most probably associated with the unequal microclimates (in particular insolation and temperature) the soil conditions and mowing regime being approximately the same..

The notable difference in post-spring flowering recorded at the South ramp site (compare 1981 with 1982) is mainly associated with the availability of moisture, in particular with the amount of precipitation during the months of September, October and November. When these months are dry (as in 1982), the dandelions do not grow so well on this sandy and sun-exposed ramp through

Table 2. Percentages of flowering heads recorded during the months of the years 1980–1982 at the 5 sites studied.

Months	South ramp			Viaduct bank			Lawn			North ramp			Pasture		
	'80	'81	'82	'80	'81	'82	'80	'81	'82	'80	'81	'82	'80	'81	'82
1–2		1	1						1						
3–4–5	90	45	85	61	99	94	47	72	70	100	100	100	90	100	100
6–7–8	2	6		7	1		16	10	23						
9–10	5	10	7	26		2	26	13	6						
11–12	3	38	8	6		4	11	4	1						

lack of water and do not manage to come into flower. It was repeatedly noted at the time that during the day the leaves were wilted owing to lack of water (through excessive insolation and relatively high temperatures). The insignificant second flowering in the Pasture must be largely ascribed to competition (for light) by the fast growing and productive grasses at this heavily fertilized site.

The causes of the differences in seasonal periodicity noted on the Viaduct bank are not clear.

A special case is the flowering strategy of lawn dandelions. A satisfactory explanation can as yet not be given, the flowering of individual plants under the moving regime in particular requiring a closer investigation. At the Lawn site the most frequent post-spring flowering was recorded in all three years of observation. The turf was intensively mowed every 7–10 days at 5 cm height. The primary effect of such frequent cutting is undoubtedly the suppression of competition by the grasses. The dandelions form a rosette addressed to the soil so that the leaves are not or only partly cut off and the capacity to produce biomass is apparently not too strongly curtailed, which means that the storage carbohydrates in the roots do not become exhausted. Conceivably the partial defoliation causes a slower rate of capitulum production. Many, but not all, flowering heads are cut off before they can produce viable achenes, and this may well be an important factor resulting in a prolongation of the formation of new heads.

3.1.4. Seasonal periodicity of flowering under uniform conditions

In order to distinguish between genetical differences as a cause of differences in periodicity and the effect of environmental factors, lots of 25 plants from all sites, the Viaduct bank excepted, were transplanted in the experimental garden and their mode of flowering was recorded (see 3.1.1). The results are shown in *table 3*.

Remarkable differences were noted. Individual plants exclusively exhibiting spring flowering were represented in the population samples from the North and South ramps by low percentages (23% and 28%, respectively), whereas in the other two (the Lawn and Pasture sites) these percentages were much higher

Table 3. Relation between seasonal periodicity of flowering of dandelion plants in relation to the number of capitula produced in the spring.

	Flowering in	Number of flowering individuals	Number of flowering individuals			
			Number of flowers per plant			
			0-14	15-29	30-44	> 45
South ramp	Springtime only	5 (23%)	3 (60%)	2 (40%)		
	Springtime and later	17 (77%)	6 (35%)	5 (29%)	4 (24%)	2 (12%)
North ramp	Springtime only	7 (28%)	6 (86%)	1 (14%)		
	Springtime and later	18 (72%)	7 (39%)	8 (44%)	3 (17%)	
Lawn	Springtime only	18 (78%)	16 (89%)	2 (11%)		
	Springtime and later	5 (22%)	4 (80%)	1 (20%)		
Pasture	Springtime only	15 (83%)	15 (100%)			
	Springtime and later	3 (17%)	3 (100%)			

(78% and 83%, respectively). It is worth recording that there is a relation with the number of heads produced in the spring. At the North and South ramp sites there is a tendency among plants only flowering in spring to produce relatively low numbers of capitula (category 0-14), whereas most of those also flowering later produce a larger number of heads in spring (*viz.*, over 14: North ramp 61%, South ramp 65%). The Lawn and Pasture population samples contained high percentages of individuals only flowering in spring, and these plants also produce relatively low numbers of heads (Lawn and Pasture 89% and 100%, respectively, in the category of 0-14 heads). These records suggest that there is a tendency towards flowering both in the spring and afterwards in individuals producing greater numbers of capitula in the spring. These plants are, generally speaking, of a larger size than the other ones. It would follow that in post-spring flowering the plant biomass plays an important role but the effect of genotypic differentiation and/or its interaction with biomass cannot be ruled out.

3.1.5. Fluctuation in the number of capitula during the main flowering period
For each biotope a comparison was made between the production of capitula in the years 1980-1982 (see *fig. 5*). The maximum number of heads (counted in the spring of 1982) was put at 100% and all the other numbers were expressed as percentages related to this maximum. It is rather remarkable that in two of the biotopes, *viz.*, at the South ramp and in the Pasture lower and about the same percentages were found in 1980 and 1981 as against a higher one in 1982 which is about three times as high. Also at the other three sites 1980 was the year with the lowest percentages of capitula but in 1981 there are differences with the South ramp and Pasture populations, the percentages recorded in that year at the Viaduct bank, the Lawn and the North ramp sites about equalling or exceeding those of the year 1982. When possible causes of the high capitulum production at the South ramp and the Pasture sites in 1982 against the low productivity in the preceding years are to be sought, management activities can

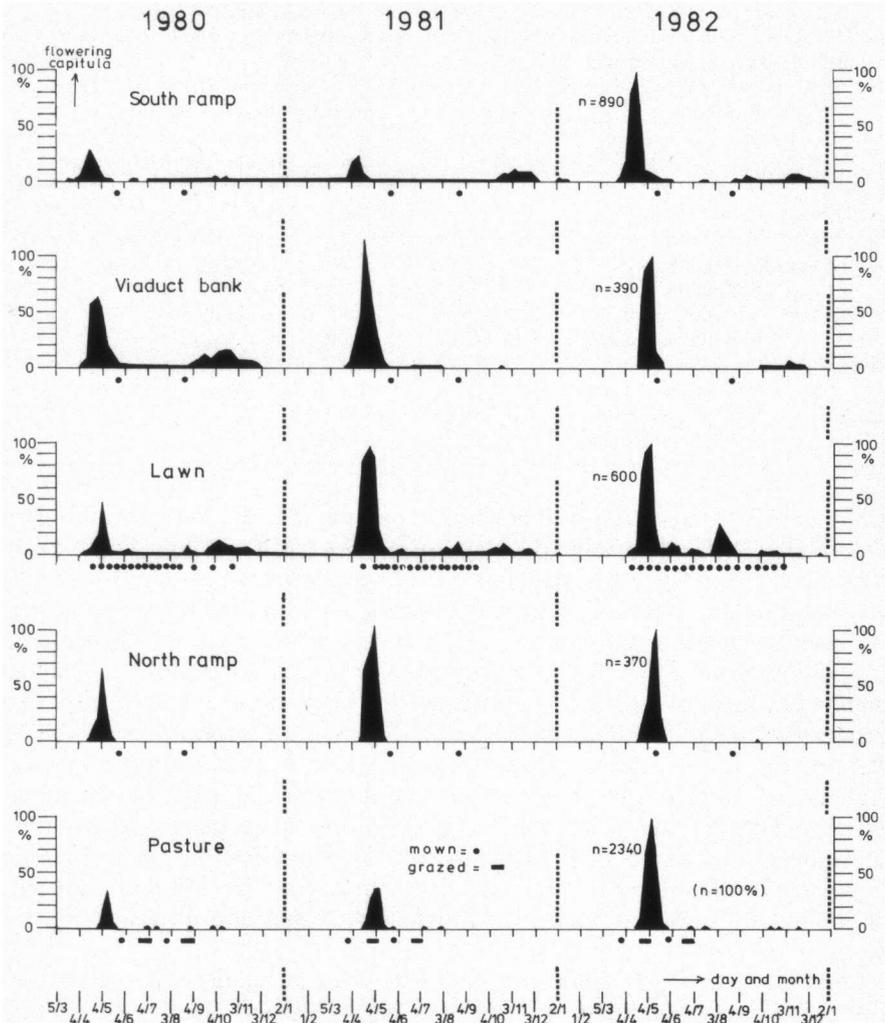


Fig. 5. Comparison of numbers of capitula of principal flowering period in 5 biotopes during 3 successive years. Maximum number of flowering capitula counted in the spring of 1982 put at 100%.

be ruled out because the dunging, grazing and mowing regime remained the same during the three years of observation. More probably the weather has something to do with it. When the rate of capitulum production is related with the meteorological date of the observation station K.N.M.I.-Schiphol, there is no correlation with the mean temperature per decade during the previous autumn, winter or early spring. Neither is there any with the total amount of precipitation per decade in the previous seasons, but there appears to be a relation with the decade sums of hours of sunshine during the months of February,

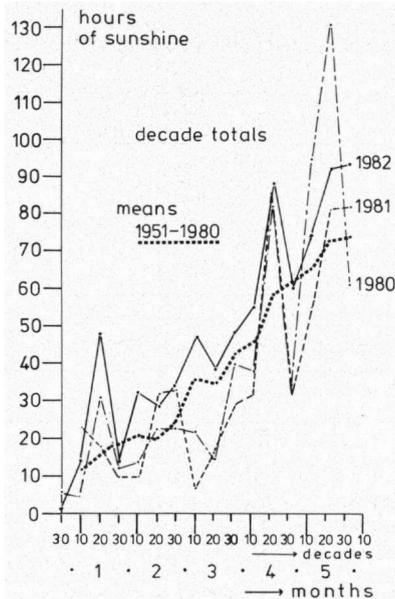


Fig. 6. Decade sums of hours of sunshine in the spring of 1980, 1981 and 1982 at Schiphol (K.N.M.I. records).

March and April. *Fig. 6* shows these decade sums for the period 1980–1982. The diagram of 1982 lies well above those of 1980 and 1981 during these apparently critical months. *Table 4* shows the monthly totals of sunshine hours and it appears that in 1982 the spring was a good deal sunnier than it was in the two preceding years.

A comparison of the radiation data with the means over a period of 30 years (1951–1980: K.N.M.I. records, 1982), see *fig 6*, indicated that 1980 and 1981 had an appreciably lower number of sunshine hours in the spring than the ‘normal’ amount during 1951–1980, whereas 1982 had more than the average.

These data suggest that for years with opulent dandelion flowering a relatively high amount of sunshine during the months of February up to April is favourable. This applies to the South ramp and Pasture sites, but in the other biotopes some additional factors must be important too, since even in the year 1981, which was poor in sunshine, a relatively high capitulum production was attained. This applies to the Lawn site, whilst at the two remaining sites the percentages of flowering heads produced were even higher than they were in the dandelion peak year of 1982. The causes are unknown but conceivably the situation at the Viaduct bank and North ramp sites is to a large extent anthropogenically determined. One may think in this connection of the adjustment height of the lawn-mowers and of the effect of road salt application, the salt being washed off into these sites. Too low an adjustment of the cropping height of the mower suppresses the competition of the surrounding grasses to a relatively large extent, whilst the influx of road salt reduces the growth rate of the grasses more strongly

Table 4. Monthly totals of sunshine (hrs.) in the springs of 1980–1982 at Schiphol Meteorological Station.

	1980	1981	1982
February	59.6	74.3	95.5
March	77.3	51.5	133.5
April	155.1	149.7	203.8
Total	292.0	275.5	432.8

Table 5. Differences in number of capitula in 1981 and 1982 of 11 plants from the South ramp.

	Nr. of plants
Less capitula in 1982	1
1–2 times as many capitula in 1982	1
2–4 times as many capitula in 1982	5
4–6 times as many capitula in 1982	4

than it does that of the dandelions.

3.2. Individual plants

3.2.1. The principal flowering period on the South ramp

The flowering phenology was studied of 11 marked plants on the South ramp during 1981 and 1982. The principal flowering flush of the individual plants showed the same trait as that of the population as a whole. The peak of bloom was attained 7 days earlier in 1982 than in 1981 (compare *fig. 1*).

Between the individual plants there are also yearly differences. The extremes, shown in *fig. 7*, are attributable to the differences in micro-habitat, although the possible incidence of genetical differences between the two microspecies *T. ekmanii* and *T. hemicyclum* (both sect. *Taraxacum*) cannot be ruled out.

3.2.2. Seasonal periodicity of flowering on the South ramp

The plants studied show marked differences in their seasonal periodicity, the principal one being between plants flowering solely in the spring and individuals also flowering later in the year. *Fig. 8* shows representatives of these two types, the highest number of capitula recorded in the spring being put at 100%. Of the 11 plants under observation 8 belong to the type of plant no. 11: *T. ekmanii* (sect. *Taraxacum*), and 3 to that of plant no. 4: *T. subditivum* (sect. *Hamata*). No attempt was made to find possible causes of this difference. There are some indications suggesting the effect of plant size on late flowering and genetical differences between the microspecies. The rate of post-spring capitulum production of plant 1 (*T. ekmanii*) was much lower in 1982 than it was in 1981. This phenomenon was noted in all plants which flowered again late both in 1981 and 1982. This agrees with the overall picture of the S. ramp population which

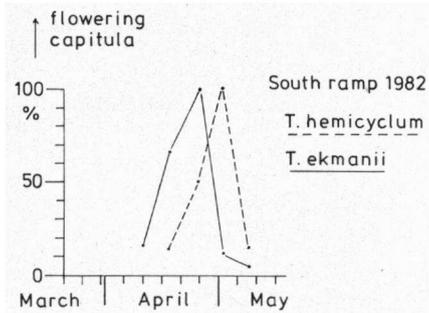


Fig. 7. The principal flowering period of 2 plants at South ramp (spring 1982) showing greatest differences (both *Taraxacum* species belong to sect. *Taraxacum*).

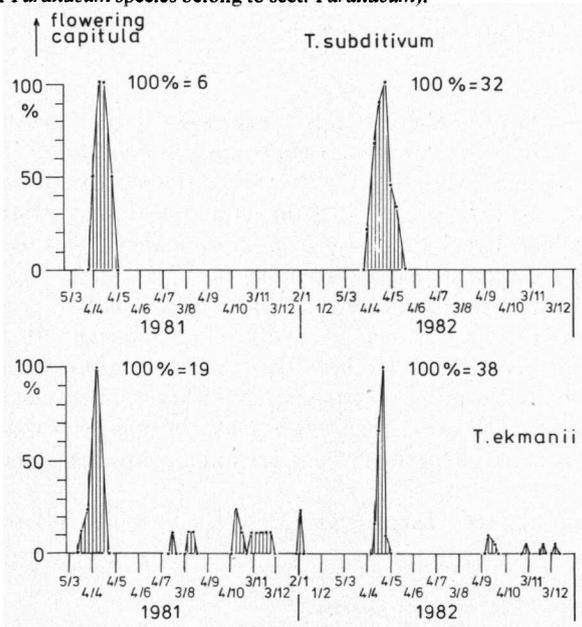


Fig. 8. Seasonal periodicity of flowering of 2 plants at South ramp in 1981 and 1982. Flowering expressed in percentage of capitula. *T. subditivum* (sect. *Hamata*) and *T. ekmanii* (sect. *Taraxacum*).

had a much less pronounced late flowering in 1982 as compared to 1981. The main reason must be sought in the drought prevailing during the months of September to November on the sunny S. ramp. That this period was unfavourable is also evident from the fact that of the 11 plants under observation three perished during that time-span.

3.2.4. Fluctuations in the number of capitula during the main flowering period
 Table 5 gives a comparison between the maximum of capitula produced by the 11 individuals under observation during the springs of 1981 and 1982.

It appears that in 1982 a decidedly larger number of capitula per plant was

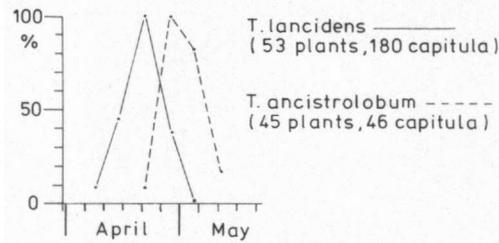


Fig. 9. The principal flowering period of *T. lancidens* (sect. *Hamata*) and *T. ancistrolobum* (sect. *Taraxacum*) cultivated under uniform conditions in the spring of 1982.

produced than they did in 1981. This agrees with the behaviour of the whole dandelion stand on that ramp (see fig. 5)

3.3. Microspecies

The spring flowering of 19 microspecies was recorded in the experimental garden in 1982. These plants were growing under uniform conditions. The flowering phenology of the taxa exhibiting the greatest difference is shown in fig. 9. *T. lancidens* (1) was the first to come into flower and also to attain the maximum. *T. adamii* (2) behaved very similarly. *T. ancistrolobum* (2) was the last to come into flower and to reach the peak of bloom; *T. raunkiaeri* (2) showed a similar pattern. Intermediate positions were taken by: *T. sellandii* (2), *T. calochroum* (2), *T. nordstedtii* (3), *T. hygrophilum* (3) and *T. hollandicum* (4). These records are indicative of genetical differences between the various taxa resulting in asynchronous main flowering. The maximum difference between the peak time of flowering is about 7 days (*T. lancidens*-*T. ancistrolobum*). However, the differences between most of the species are smaller and the flowering times show much overlapping.

(1): sect. *Hamata*, (2): sect. *Taraxacum*, (3): sect. *Spectabilia*, (4): sect. *Palustria*.

4. CONCLUSIONS AND DISCUSSION

When in the present paper populations of dandelions are mentioned, only the reproductive individuals present in the square sample plot are intended. Since in each biotope studied several microspecies occur sympatrically, these populations contain several dandelion taxa. This unusual concept of 'population' was chosen because it is virtually impossible to identify the hundreds to thousands of individuals forming a population to the microspecies level and to record the phenology of each microspecies separately.

The results of our survey renders it clear that the flowering phenology of dandelions, both at the level of populations and as individual specimens, varies appreciably in different biotopes. As emanates from the discussion of the results, there are apparently two principal causes of the differences between the course of the main flowering period and the seasonal periodicity, viz.,

- (a) varying environmental factors, and
- (b) genetically controlled differences between microspecies and possibly even within a single one; conceivably both causes often operate in combination (a + b).

That genetic differences between the microtaxa do exist has become clear from the transplantation experiment when different microspecies were reared under uniform conditions. The maximum time difference between the peaks of spring flowering appeared to be about 7 days, but the differences between most of the taxa were much smaller. The situation regarding *T. ancistrolobum* agrees with the report by HAGENDIJK et al. (1982) that this taxon comes into flower later by about a week than most other members of sect. *Taraxacum*. Data relating to other Dutch dandelions are wanting.

These findings correspond with those of HOFSTEN (1954), who studied the anthecology of a number of microspecies of sect. *Taraxacum* in great detail in Sweden. He reports a difference in the time of commencement of spring flowering of up to 13 days, but most of the taxa studied showed an almost complete coincidence of their flowering times. In Sweden (surroundings of Uppsala) the dandelions of sect. *Taraxacum* flower from the end of May till the end of June, i.e., a little over a month later than in The Netherlands.

It is remarkable that we did not record any significant differences between the main flowering periods of the microspecies of the sections *Spectabilia* (*T. nordstedtii* and *T. hygrophilum*) and *Palustria* (*T. hollandicum*) from relatively undisturbed habitats on the one hand and those of the sections *Hamata* and *Taraxacum* from disturbed ones on the other. The flowering time of the microspecies of the first mentioned sections coincided most with those of *T. calochroum* and *T. sellandii*, which occupy an intermediate position within the flowering spectrum of sect. *Taraxacum* as far as examined. The microspecies of sections *Spectabilia* and *Palustria* are at home in moist biotopes in which the temperature starts rising relatively rather late and also attains higher values later than in the biotopes of the representatives of sect. *Taraxacum* studied. Most probably the flowering times of the microspecies of sections *Spectabilia* and *Palustria* found in wetter and colder habitats are mainly regulated by the environmental conditions (primarily the temperature). Generally speaking one may conclude that the genetically controlled differences in spring flowering observed in representatives of *Taraxacum* are small and strongly overlapping.

A comparison of the flowering strategy of natural populations with that of plants grown in the experimental garden under uniform conditions revealed that the environment (chiefly the temperature) is mainly responsible for the mode of flowering. According to HOFSTEN (1954) especially the soil temperature is of importance.

The spring season is clearly the most important flowering period. In some biotopes late flowering occurs but rarely or not at all but in other habitats late flowering is of regular incidence and sometimes takes place on a rather large scale. This agrees roughly with data recorded by GRAY et al. (1973) who report that in Kentucky (U.S.A.) a second concentration of blooming individuals oc-

curs in September till the beginning of October. In some localities in The Netherlands flowering individuals may be present even in winter, which agrees with the findings of GRAY et al. (1973). Lawns constitute a special case in this connection because in this habitat late flowering takes place most frequently.

Generally speaking the number of capitula produced in the summer and autumn is decidedly lower than that produced in the spring flush of blooming. This is attributable to two circumstances, viz., (a) because not all plants which flowered in the spring come into flower again later in the year, and (b) because the mean number of heads produced per plant is also lower after the main flowering period in spring. There are, furthermore, some manifest indications of the importance of plant size (biomass) in this connection. At some biotopes with a relatively low rate of competition dandelions may attain a very large size and produce several shoots with many leaves and heads (ramps), whereas in other ones the individuals remain much smaller (pastures: competition with grasses and other herbs). This may have some bearing upon the phenomenon that ramps upon the whole exhibit a higher rate of late flowering than, e.g., pastures.

An important observation is the fluctuation in the number of capitula produced in different populations during three consecutive years. Generally speaking fluctuations in populations are complex phenomena, several processes contributing to the variation in intensity, etc. The production of flower heads of a population is decided by the stand density of the flowering dandelions on the one hand and by the number of heads borne per plant on the other. Both parameters may up to a point vary independent of one another because they are induced by mostly different ecofactors. A preliminary investigation into these phenomena was carried out especially at the South ramp site. Of the 11 individuals kept under observation the number of heads produced in 1982 was twice to six times as high as it was in 1981. This implies that the increased capitulum production of the whole population in 1982 can be explained by an increased fertility of the plants already present at the site the year before (in 1981). The increase is, therefore, not the primary result of an increase in stand density although this may also have had some effect.

Other populations have not been studied in this way. The amount of heads produced per plant depends on a number of factors, the factor light intensity being of paramount importance. A study by LISTOWSKI & JACKOWSKA (1965) has shown that dandelions (*T. officinale*) may come into flower in a great range of light regimes, both as regards day length and radiation intensity. *T. officinale* belongs to the category of the photoperiodically neutral plants, but relevant pertaining experiments revealed that a short-day regime stimulates flowering. The combination cold period – short-day regime results in the highest rate of capitulum production. LISTOWSKI & JACKOWSKA (1965) also found that, apart from the day length, the light intensity has a considerable effect upon the flowering behaviour, low intensities resulting in much lower percentages of flowering individuals or in a total inhibition of flowering. It must be borne in mind that flowering induction and bud initiation are very important processes for the flowering phenology. These processes take place in the previous autumn and win-

ter.

According to VAN LOENHOUD & VAN DER HEIJDEN (1980) the tap-root size in the autumn to an appreciable extent also decides the size of a dandelion in the following spring and the number of heads produced. This means that also the environmental conditions prevailing during the preceding summer and cold season have an appreciable bearing upon the flower production during the next spring.

Conceivably more heads are being initiated in a favourable autumn and a greater amount of the potential buds develops into a head in a favorable spring than in a more inclement one. This requires a closer investigation.

Only populations of (as far as can be ascertained) obligatorily agamospermous triploids were included in the present investigation. In these microtaxa pollen production is not at all essential for their reproduction. This explains why a few agamospermous Dutch ones (which constitute a small minority) do not produce any pollen at all (HAGENDIJK et al. 1982). It is noteworthy that such apolliniferous forms, as far as studied, do not differ from the pollen-producing ones in their flowering behaviour. The capitula and the individual florets of most of the agamospermous dandelions have an (almost) completely normal morphology and are also normal in other respects such as the production and extrusion of pollen, nectarial secretion, protandry, the exposure of the stigmatic surfaces of the recurving stigmatic lobes, etc. According to MAYNARD SMITH (1978) this must be explained by the relatively very young phylogenetic age of these forms. There are circumstances when also in microtaxa with obligatory agamospermy pollen production may be important. Such is the case when diploid sexual individuals (biotypes) and/or triploid and facultatively agamospermous ones occur sympatrically with obligatorily agamospermous populations. (Incidentally?) the obligatorily agamospermous forms may act as pollen donors which may conceivably result in fertilisations of sexual and/of facultatively agamospermous individuals. This possibility has been experimentally shown to occur by RICHARDS (1970b) and JENNISKENS (in prep). In this way hybridisation and introgression may result in the advent of new agamospermous clones and possibly even novel microspecies. This process may thus account for a good deal of genetical and evolutionary flexibility within the agamous complex *Taraxacum*. If this is in nature the case, there must be a positive selection for pollen production and synchronisation of flowering of obligatorily and facultatively agamospermous triploids, and diploid sexual forms.

This is also of importance in The Netherlands since recently diploid and sexual dandelions have been recorded and the occurrence of facultative agamospermy in triploids is deemed possible (STERK et al. 1982).

In connection with the flowering of the obligatorily agamospermous triploid not only gene flow and hybridisation are of importance but also the subsequent seed production. There are indications that the sexual diploids only flower in spring and set seed only once, whereas triploids may also do so later in the year. This may signify that from the viewpoint of population dynamics the diploids are in a somewhat less favourable position on account of a lower total annual

achene production than the triploids with late flowering. One must bear in mind that in this country di- and triploids are almost always found sympatrically in a single habitat (a meadow). In order to counteract the ousting-out by triploid forms, the diploids must have some advantage over the triploids or occupy other niches. An alternative possibility is that owing to continual hybridisations in the same biotope diploid and triploid forms arise anew. These points are under investigation.

ACKNOWLEDGEMENTS

We express our gratitude to Rijkswaterstaat, Dienstkring Bussum, for their co-operation as regards the investigation on the ramps of motorway A9; to Mr. B. de Vries (Abcoude) for permission to study *Taraxacum*-populations in his pasture; to Ms. G. M. v.d. Heijden for technical assistance; to Dr. J. C. M. den Nijs for fruitful discussions. The diagrams were drawn by Mr. G. Oomen and Miss C. J. J. Diesbergen did all the typing. Professor A. D. J. Meeuse critically read the original draught and is responsible for the English translation. The authors wish to express their sincere indebtedness for all kind co-operation.

REFERENCES

- FILMER, R. S. (1941): Honeybee population and floral competition in New Jersey Orchards. *J. Econ. Ent.* **34**: 198–199.
- FREE, J. B. (1968): Dandelion as a competitor to fruit trees for bee visits. *J. Appl. Ecol.* **5**: 169–178.
- FÜRNKRANZ, D. (1960): Cytogenetische Untersuchungen an *Taraxacum* im Raume von Wien. *Oesterr. Bot. Z.* **107**: 310–350.
- GRAY, E., E. M. MCGEEHEE & D. F. CARLISLE (1973): Seasonal variation in flowering of common dandelion. *Weed Science* **21** (3): 230–232.
- HAGENDIJK, A., J. L. VAN SOEST & H. A. ZEVENBERGEN (1975): *Taraxacum* (behalve sectie *Vulgaria*). *Flora Neerl.* **IV** (9): 1–52.
- (1982): *Taraxacum* (sectie *Vulgaria*). *Flora Neerl.* **IV** (10a): 79–150.
- HEUKELS, H. & S. J. VAN OOSTSTROOM (1977): *Flora van Nederland*. Groningen. 19th ed. 925 pp.
- HOFSTEN, C. G. (1954): *Studier över släktet Taraxacum Wigg. med särskild hänvisning till gruppen Vulgaria Dt. i Skandinavien*. Thesis Stockholm. 432 pp.
- JENNISKENS M. J. P. J. (in prep.) *Hybridization in diploid sexual plants of Taraxacum (sect. Taraxacum) in Central Europe*.
- K.N.M.I. (1982): Climatological data of stations in the Netherlands. *No 10. Normals and standard deviations for the period 1951–1980*. De Bilt. 118 pp.
- LISTOWSKI, A. & I. JACKOWSKA (1965): Observations on plant development XI: On the rhythm of flowering of *Taraxacum officinale*. *Act. Soc. Botanicorum Poloniae* **34** (3): 549–561.
- LOENHOUD, P. J. VAN & G. M. VAN DER HEIJDEN (1980): Flowering strategies in *Taraxacum*. *Act. Bot. Neerl.* **29** (2/3): 207.
- LONDO, G. (1977): *Natuurtuinen en -parken*. Zutphen. 134 pp.
- (1983): Over de indicatieve betekenis van de groeiwijze en de bloei van plantesoorten. *Natura* **80** (5): 233–236.
- MAYNARD SMITH, J. (1978): *The Evolution of Sex*. Cambridge. 222 pp.
- ØLLGAARD, H. (1983): Hamata, a new section of *Taraxacum* (Asteraceae). *Pl. Syst. Evol.* **141**: 199–217.
- PERCIVAL, M. S. (1955): The presentation of pollen in certain angiosperms and its collection by *Apis mellifera*. *New Phytol.* **54**: 353–368.

- RICHARDS, A. J. (1970-a): Eutriploid facultative agamospermy in *Taraxacum*. *New Phytol.* **69**: 761-774.
- (1970-b): Hybridization in *Taraxacum*. *New Phytol.* **69**: 1103-1121.
- SOLBRIG, O. T. (1971): The population biology of dandelions. *Amer. Sci.* **59**: 686-694.
- STERK, A. A. (1982): Inleiding tot het geslacht *Taraxacum* in Nederland. In : A. HAGENDIJK, J. L. VAN SOEST & H. A. ZEVENBERGEN (1982) *Taraxacum* (sectie *Vulgaria*). *Flora Neerl.* **IV** (10a): 53-77.
- , J. C. M. DEN NIJS & W. KREUNE (1982): Sexual and agamosperous *Taraxacum* species in The Netherlands. *Acta Bot. Neerl.* **31** (3): 227-237.
- , M. C. GROENHART & J. F. A. MOOREN (1983): A study of the ecology of some microspecies of *Taraxacum* in The Netherlands. *Act. Bot. Neerl.* **32** (5/6) 385-415.
- WESTHOFF, V. & A. J. DEN HELD (1975): *Plantengemeenschappen in Nederland*. Zutphen. 324 pp.