Observations on plant development. XI

On the rhythm of flowering of *Taraxacum officinale*

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Taraxacum officinale, a common perennial plant, multiplies both generatively and vegetatively. In natural conditions it flowers profusely in May and June (Szafer 1924), and again though much less intensively in early autumn (Tymrakiewicz 1959).

Observations on the flowering of this plant were made twice under different light conditions and time of seeding in the periods 1957—1960 and 1963—1964. In the first group of experiments the progeny of plants collected in the environs of Gorzów Wielkopolski served as starting material, in the second group plants from the Puławy region. The "Gorzów" population was more homogeneous than that from Puławy. In the second group wide individual variations occurred in the size and incisions of the leaves. Plants with lighter-coloured and less indented leaves, with wider and more rounded lobes and smaller number of leaves, set the first bud somewhat later under e.g. conditions of lower light intensity. The differences observed do not, however, exceed the limits of variation within one — relatively polymorphic — species (Hegi 1931).

The results of observation of the "Gorzów" population carried out in the period 1957—1960 have been reported in one of the previous publications (A. Listowski and A. Jeśmianowicz 1960) therefore only general data will be repeated here.

Plants sown on Sept. 7 in a glasshouse and grown under continuous, natural and short daylight all flowered between the 140th and 240th day from germination. Further observations were made on plants sown at various dates: Apr. 17, May 19, June 3, July 5, 1958. Part of the plants remained the whole winter out-of-doors, and part was transferred in autumn to the glasshouse under continuous (natural + illumination with 200 W Osram bulb) and short (natural reduced when necessary to 8 hr) daylight.

The course of flowering in all the groups is illustrated by Graph 1. The results proved that the plants can flower within a very wide scope of conditions. However, the age at which the plants passed to the

Graph. 1. *Taraxacum officinale*. Percent of flowering plants by different light conditions and different sowing time

generative phase and set their first bud differed and was dependent on the light conditions. Under strongly weaning light conditions efflorescence was retarded. In plants which came into bloom in early autumn, the process was mostly interrupted for a longer interval in late autumn. The course of the curves illustrating summarily the number of plants flowering (both for the first and second time) show a somewhat greater frequency of efflorescence under short than under continuous light.

On the date of "maximum" flowering frequency, the percentage of efflorescent plants and the duration and intensity of flowering are higher under short day.

This may be ascribed to a certain stimulating influence of short-day conditions. Vernalization is not indispensable for flowering, its influence is, however, significant.

Part of the plants sown in 1958 at various dates were left outside for the winter. Notwithstanding the seeding dates and the fact whether the plants came into flower before the winter, they all flowered in May of the following year. The rhythm of efflorescence — as far as coming into bloom of particular plants and the length of their flowering period are concerned — was much more uniform than in the plants kept in the glasshouse. Thus low temperature seems to have an intensifying effect on flowering, and under the influence of vernalization, the individual differences in the term, length and intensity of flowering seem to be attenuated.

Although the plants seeded at any date between April and July came into bloom generally at the same time, the age of the plants seems, nevertheless, to play a certain role. Plants of the 1st group sown on September 7 kept in the glasshouse in winter began to flower in February. The maximum number of flowering plants was recorded in April.

The plants left outside were at the beginning of winter in the phase of a very young rosette (c. 4—5 leaves). They did not flower in April—May only towards the end of summer.

This seems to indicate that plants must reach a certain age limit, associated with differentiation of a certain number of leaves, and consequently, with attainment by these leaves of a maximum physiological activity, to make the process of flowering possible. A too early exposure to vernalization gives no effect.

Since in the experiments of 1958/1959 the rhythm of inflorescence of the particular plants in the given experimental combination was not recorded, further observations were made in the period 1963—1964 on the progeny of several plants growing near the glasshouse in Puławy.

The experiments were carried out in several variants:

Variant (a). Seeding date Oct. 19. Early and uniform sprouting.

Graph 2. Period of bud formation in plants grown under normal day length (N₁), short day (S₈) and continuous light (L₂₄) conditions in the growth chambers

Graph 3. Periods of bud formation in some plants transferred on March 20 under continuous light conditions after 150 days of growth under light of natural day length (sowing date October 19)

At the phase of 2 leaves the plants were transferred to light chambers where they grew under continuous light (L_{24}), long 16-h day (L_{16}) and short 8-h day (S_8). Glow tube light of 4000 Lux was applied. Temperature in the chambers varied within 20—24°C.

Observations were made to July 27 when the experiments were interrupted.

Variant (b). Parallely to the group of plants growing in the light chambers, another group seeded on Oct. 19 was grown in the glasshouse under naturally varying daylength, first short and of weak intensity, and after the New Year rising gradually in length and intensity.

At the end of March the plants of this group (N) were divided into three parts: one was left under natural rising daylight, in the second the plants were shaded at 3 p.m. so that night began for them in the early afternoon ($N \rightarrow S_8$), the third group was exposed to continuous illumination (natural + 500 Watt bulbs in the hours of darkness) ($N \rightarrow L_{24}$).

Variant (c). The plants grew under natural daylight and under the same with shading from 3 p.m. similarly as in variant (b) only they were sown later (Nov. 15, Dec. 15, Jan. 19).

The plants in variants (b) and (c) were observed till November 1964.

In all experiments the following data were recorded: setting of the first bud, number of leaves developed up to date; number of green leaves present on the plant, date of appearance of further buds and date of their coming into flower.

The results of these observations are summarized in Tables 1 and 2.

Graph 2 gives a certain number of "spectra" of the efflorescence of the particular plants differing in the rhythm of flowering.

It should be borne in mind when drawing conclusions that:

a) plants growing in the light chambers grow under conditions of reduced light quantity as compared with group N.

b) the groups L_{24} , L_{16} and S_8 in the chambers differ by the amount of light received which in the case of S_8 is particularly low.

c) plants under L_{24} in the chamber receive much less light than those growing under long summer daylight, since they are illuminated in the night with light of low intensity.

The reactions observed are, therefore, the result of the interaction of the "light conditions as a whole" and not of daylength solely.

Table 1

Variant „a”, Sowing date October 19

Setting of the first bud	No. of days from sowing	2/I	13/I	20/I	5/II	14/II	20/II	28/II	9/III	18/III	27/III	2/IV	13/IV	22/IV	28/IV	No. of plants		Age of plants at the begin. of flow.	No. of leaves at the begin. of flower.*		Total No. of buds (Mean) and (Min-Max) *	Duration of flow. (days) *	
		total	flower. %	total	flower. %	total	flower. %	total	flower. %	total	flower. %	total	flower. %	total	flower. %								
L ₂₄	3	85	96	103	119	128	134	142	151	157	169	175	186	195	201	42	34	80	85—186	87	64 (46—101)	41 (14—76)	101 (38—126)
L ₁₆	1		13	1	9	5	1	3	0	0	0	1	0	0	0	42	34	80	85—175	96	72 (51—90)	12 (2—31)	47 (12—119)
S ₈	—		—	—	—	1	1	0	1	8	4	5	6	1	1	40	28	70	128—201	105	75 (45—85)	4 (1—10)	21 (8—25)
N	—		—	—	—	—	2	6	4	10	8	7	3	0	0	40	40	100	134—186	55	41 (29—54)	65 (26—167)	130 (75—145)

* Mean and in brackets: minimal and maximal numbers.

Table 2

Variants b, c, Sowing date October 19, November 19, December 19, January 19

Sowing date	Combination	Setting of the first bud		Age of plant at the begin. of flower		% of flow. plants	No. of leaves at the beg. of flow.*		Total No. of buds*	Duration of flower. (days)*
		from	to	from	to		total	green		
19.X	N	20.II	13.IV	134	186	100	55 (39—73)	41 (29—54)	75 (33—118)	164 (79—247)
19.XI	N	25.III	20.V	126	183	100	72 (60—118)	55 (30—84)	38 (9—111)	84 (37—170)
19.XII	S ₈	2.IV	4.V	136	166	100	66 (43—118)	51 (31—86)	40 (10—72)	91 (22—171)
	N	25.III	16.V	96	149	100	63 (48—93)	50 (33—72)	45 (8—139)	101 (43—178)
	S ₈	2.IV	4.V	104	137	100	55 (38—75)	44 (20—63)	45 (7—109)	95 (25—146)
19.I	N	14.IV	2.VII	85	164	100	79 (28—152)	64 (26—108)	30 (11—104)	63 (9—177)
	S ₈	14.IV	22.VI	85	154	100	54 (23—134)	45 (22—96)	30 (6—94)	85 (22—155)

* Mean and in brackets: minimal and maximal numbers.

PLANTS IN LIGHT CHAMBERS

Combination L_{24} . The wide individual variations are evidence of the segregating effect of light conditions. A part of these plants flowered earliest of all, often with a smaller number of leaves than in the remaining two groups, but the dates of efflorescence show a wide dispersion and part of the plants did not come into flower to the end of July.

The frequency and number of buds set is highest and the time of flowering relatively the longest.

Group S_8 . The behaviour of the plants is opposed to that in the foregoing group. Setting of buds is delayed but the average number of leaves is higher. The bud-setting frequency is lowest and the period of flowering not continuous.

Group L_{16} occupies an intermediate position between the other two. In combinations L_{16} and S_8 a part of the plants did not come into flower to the end of July. This may be ascribed, in contrast to the "nonflowering" plants of combination L_{24} , to the effect of too small an amount of light (observations interrupted on July 27). After this date the plants which had not bloomed were placed for several hours daily under natural daylight and they all flowered.

Plants growing under natural daylight of varying length (N).

Plants seeded on Oct. 19 showed a delayed setting of the first bud (under short day at this date and low-intensity light) as compared with the plants grown in the chambers under L_{24} and L_{16} . In time the process of flowering became quicker and quicker and all the plants came into bloom. The number of leaves at the moment of efflorescence is the lowest, the period of flowering the longest and budding most intensive as compared to the plants growing in the chambers under L_{24} .

Plants from the later seeding dates (Sept. 19, Dec. 19, Jan. 19) also all came into flower. The first flowers appeared the earlier the later was the date of seeding. However, the period of flowering was shortened and a certain decreasing tendency could be observed in the intensity of flowering. It would seem, as indicated by comparison of the indexes for the plants sown on January 19 with those from earlier seeding dates, that the initial induction with short day together with the still weaning tendency of the light conditions is more favourable for intensive flowering than growth from the very beginning under rising light conditions ($S \rightarrow L$).

DISCUSSION

Rhythm of flowering. The dates of appearance of the successive buds, of their coming into flower and overblowing were recorded

for each plant. The results gave a picture of the rhythm of individual flowering.

It is neither possible nor necessary to present here the results for all the material, it seemed, however interesting to present the "types" of spectra on the example of some selected plants (Graph 2).

In general the following "types" of flowering rhythm could be distinguished:

a) plants flowering early and long. Florescence continuous or only short intervals between the formation of the successive buds. Frequently more than one bud at a time is formed;

b) plants coming into flower with delay or flowering early but for only a short period. Florescence continuous and budding often intensive;

c) plants beginning to flower early, the process is, however discontinuous, several longer intermissions alternating with flowering occur;

d) plants setting the first bud early or somewhat later, budding intensity low in general, intervals between appearance of successive buds very long, the flowering period mostly short. Examples:

In combination L_{24} growing in light chambers plants of types a, b and c were observed:

type a) 100—160 days of florescence, 27—56 buds in this period. Of the 34 plants coming into flower, about 15 may be classified to this group.

type b) nine plants, average period of flowering 40—50, rarely up to 100 days. Number of buds set 9—37. End of florescence in mid June or earlier.

type c) ten plants, 24—46 buds, intermissions of 2—3 weeks in flowering.

In combination L_{16} most plants set the first bud early, their florescence, however, ended quickly, e.g. in the first days of March. Only about 10 of the 34 flowering plants set buds later after shorter or longer intermissions.

In combination S_8 type "d" dominated. In part of the plants, after early formation of even more than one bud, the intermission lasted 4—6 weeks or more. Only few plants flowered more intensively.

In conditions N, the most frequent is type "a".

These rhythms point doubtlessly to a dependence on light conditions. The frequency of bud setting is apparently regulated by a quantitative process of threshold character.

On the other hand, individual differences in the rhythm of bud setting (see Graphs 2 and 3) seems to be the expression of segregation occurring in the experimental group which may be considered as a differentiated population in respect to "optimum" and "critical" light conditions.

This differentiation becomes manifest in nonoptimum (for interaction of daylength and light intensity) light conditions. The differences are smaller with spring seeding dates (see Graph 1, seeding Agr. 17), and almost completely disappear when the plants pass the winter in natural conditions coming into flower in May and June. This obliteration of individual differences was observed in the experiments of 1957/1958 in which — after natural vernalization — the term and intensity of flowering were equal, notwithstanding the date of sowing.

Influence of daylength and light intensity

As may be concluded from observation, *Taraxacum* flowers within a very wide amplitude of variability both of daylength and light intensity.

The plant might therefore be classified as belonging to the photo-periodically neutral type. On the other hand, within the framework of interrelations between varying daylength and different light intensity, there occur not only wide variations in the intensity of florescence and frequency of bud setting in the plant which has once come into flower, but also differences in the date of flowering of the particular plants and the length of flowering in the given combination.

Under natural daylight flowering is most uniform and intensive:

This is true above all in the case when the plants are seeded in autumn, pass a certain period under short and weaning daylight which then gradually increases. Shortening of this period of "low-level light conditions" (e.g. by sowing in January) reduces the intensity of florescence. If the day is shortened (in the early afternoon) for plants sown in spring or early summer and growing under natural light, the effect (as seen from Table 2) is rather favourable, the uniformity of flowering and frequency of budding are increased. In the experiments of 1957/1958, the number of flowers coming into bloom was always somewhat higher under short day.

The fact would rather seem to point to a certain stimulation and intensification of florescence under the influence of short day, both as a following effect on plants growing in their youth under short day, and under reduced daylight applied to plants already flowering and grown under conditions of summer long day.

The behaviour of the plants in the light chamber contradicted this tendency. Under low-intensity light, the leaves of the plants exposed in the chamber to short day differentiated more intensively, and at the same time budding was delayed. The intensity of florescence was greatly reduced (see Graph 2). Under continuous illumination, on the other hand, the intensity of flowering was markedly higher as compared with that under 16-hour day, and the dates of flowering were mostly

earlier. If related to the average of the whole population, continuous daylight of low intensity shows a distinct intensifying effect on the process of flowering as compared to that in experimental populations growing under L_{16} and still more so under S_8 . However, a large proportion of the plants under continuous illumination did not come into bloom.

Thus in the chambers both a part of the plants under short and under continuous daylight did not flower.

The reasons for this, seem, however to be different; in the first case florescence is inhibited by the insufficient amount of light, and in the other by an excess of light above a certain "maximum". The critical thresholds for the "minimum" of the absolute light quantity as well as for the inhibitory "maximum" under continuous daylight show a distinct variation from plant to plant.

The restricting or inhibitory influence of continuous illumination is manifest in the experiments of 1957/1958 (Graph 1) in the lower frequency and shorter period of flowering.

This influence was most evident when part of the plants seeded on Oct. 19, grown and flowering under natural light were transferred to continuous light conditions (weak illumination with 400 W from sunset till morning). Most of these plants (but not all) soon ceased to flower (see Graph 3).

Summing up all the observations, it may be stated that: both under short and continuous day interacting with light intensity, conditions intensifying as well inhibiting the process of flowering were observed.

Short day (8 hours), with light intensity specific for natural conditions in this country in spring and summer, seems to prolong the period of flowering and intensify florescence in the sense of reducing individual variations (shift towards facultative short-day reaction).

Continuous illumination, i.e. long natural day supplemented with relatively weak illumination during the night hours has a rather weak inhibitory effect showing wide individual variations.

Natural varying daylight in the $S \rightarrow L$ sequence seems most favourable as regards intensity and uniformity of florescence, provided the short day phase lasts longer exerting a following effect.

Plants which start growth under long day come into flower in autumn that is under weaning daylight. Vernalization seems to be a factor activating the process of flowering and levelling the individual differences and thus reducing the modifying effect of light conditions.

Thus the seemingly simple "neutral photoperiodic" reaction of *Taraxacum* proves to be more complex under closer analysis and subject to major modifications. The occurrence of such modifications of "funda-

mental" type in the photoperiodic reaction in dependence on interaction with temperature, light intensity and quality have already been the subject of some observations among which the numerous works of Mathon and col., 1962, should be mentioned. They describe a number of "transformation" models of photoperiodic type occurring in one and the same plant in dependence on the interaction of daylength with light intensity or quality. Particularly worth attention here are observations on the soy bean which comes into flower when exposed to long day of low intensity (Gallochet 1962), and those of Wellensick (1960) who demonstrated that in the typically SDP *Salvia occidentalis*, the inhibitory influence of light may be abolished by diminishing its intensity. In such a case *Salvia occidentalis* comes into flower normally under continuous daylight. Thus, a change of distinctly photoperiodic type occurs here (in the sense of the terminology used so far).

The authors' own observations indicate that the effect of varying daylight as compared to illumination for a fixed period of hours is more favourable or even quite different (Listowski, Jackowska 1964).

The modifications favourable to flowering occurred in *Taraxacum* under light conditions varying both from S to L and L to S, in dependence on the interaction with light intensity.

As regards flowering under natural conditions, this occurs under maximum light intensity in May and June and again but less intensively in early autumn (Hegi, Tymrakiewicz).

The following conclusions may be drawn from the present observations:

a) plants germinating in summer — from seeds disseminated in spring — partly come into bloom in the same vegetative season. The first bud may appear at various times and one cannot speak of any more or less distinct leaf index which would characterize ripeness to flowering. It can only be stated that in the juvenile (exclusively vegetative) phase at least 20—23 leaves develop but the upper limit may be very high reaching as much as 100 leaves or more;

b) plants which bloomed already once in spring come into flower again in autumn. Bud formation in these plants occurs in the period of weaning daylight. The differentiation of new leaves is limited and those developed previously show symptoms of premature ageing. It is at this stage that buds develop.

Obserwacje nad rozwojem roślin. XI.
Rytm kwitnienia Taraxacum officinale

Streszczenie

Taraxacum officinale — można zaliczyć do roślin fotoperiodycznie neutralnych. Rytm kwitnienia, jak i jego intensywność ulega jednak dużym modyfikacjom przy różnych układach długości dnia i natężenia światła.

Dzień krótki w warunkach wysokiego (naturalnego) natężenia światła stymuluje kwitnienie. Na niskim natężeniu — na odwrót — intensywność kwitnienia jest niska.

Dzień ciągly — przy wysokim natężeniu raczej hamuje kwitnienie — przy niskim na odwrót.

Dzień zmienny — byłby najkorzystniejszy z punktu widzenia intensywności i równomierności zakwitania.

Wahania międzyosobnicze rytmu kwitnienia duże, można wyróżnić tu pewne typy (wykres 2 i 3).

REFERENCES

- Gaillochet J., 1962, C. R. d. Séances de la Soc. de Biologie 156:11.
Hegi G., 1931, Illustrierte Flora v. Mitteleuropa VI. Z. 1088.
Listowski A., Jeśmianowicz A., 1960, Roczn. N. Roln. 81, 2.
Listowski A., Jackowska I., 1964, Acta Soc. Bot. Pol. 33:4.
Mathon Ch. Cl., Stroun M., Grossin F., Gaillochet J., Gandrieu A., 1962, 87-Congres des Soc. Savantes.
Szafer Ch. Cl., 1963, Activité du Service d'Ecophysiologie (CNRS).
Mathon Wl., 1924, Rośliny polskie.
Tymrakiewicz W., 1959, Atlas chwastów.
Wallensiek S. J., 1960, CR. de l'Acad. d'Agric. de France 10:607.