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Photoperiodic and thermal requirements for the flowering of *Bryophyllum daigremontianum* (Hamet. et Perr.) Berg. and *Bryophyllum tubiflorum* Harv.

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Abstract

Marked differences were found between the photoperiodic responses of *Bryophyllum daigremontianum* and *Bryophyllum tubiflorum*, both species being classified as long-short-day plants (LSDP). The flowering of *B. daigremontianum* was observed under several photoperiodic conditions, among others under continuous exposure to long day (LD) or after transferring plants from a short-day (SD) to a long-day exposure: both conditions were regarded previously as non-inductive. It is argued that the flowering of *B. daigremontianum* is conditioned by sufficiently long LD exposure followed by one of two factors: the shortening of the day or the lowering of the temperature. The flowering of *B. tubiflorum* was observed only under more specific photoperiodic conditions, it seems to be conditioned by several successive changes of the length of the photoperiod.

INTRODUCTION

Some species of *Bryophyllum* (*B. daigremontianum*, *B. tubiflorum*, also *B. crenatum*) were classified as long-short-day plants (LSDP) which form flowers only after exposure to long day followed by short day or after treating them with gibberelline under SD conditions (Dostál, 1949; Resende, 1952; Bünsow, Harder, 1956; Penner, 1960; Zeevaart, Lang, 1962; Michniewicz, Lang, 1962; Marcelle, 1971). The flowering of *B. daigremontianum* can also be obtained by grafting together two noninducted components: a scion growing in LD upon stock growing in SD (Chailakhyan, Yanina, 1971, 1973). According to the authors mentioned above, the exposure of plants to

LD or to SD conditions only, will not result in the flowering of *Bryophyllum.* Only Resende (ref. Penner, 1960) reported on (delayed) flowering of *B. daigremontianum* under constant daylength when it was close to the critical value.

The thermal requirements of floral induction of *Bryophyllum* were determined in only a few papers. Zeevaart and Lang (1962) have suggested that the transfer of plants from LD to SD conditions or treatment with gibberelline in SD would result in flowering only on condition that the temperature in the night does not exceed 15°C. Detailed studies of Van de Pol (1972) showed that plants come in to flower only "when the sum of the products of the temperature times hours per 24 hours is 472 or less" whereas a lowering of temperature during the period of darkness is not necessary. Moreover, Van de Pol suggested that high temperature does not influence the development of the floral induction produced by a short or long day, it destroys, however, the existing level of floral hormone.

During my preliminary investigations of the flowering of *Bryophyllum* I have found significant differences from the findings reported by other authors. Taking into account that studies on LSD plants flowering (depending both on short and long day induction) were expected to explain the mechanism of flowering in general, and that these studies were carried out mainly on *Bryophyllum,* it seemed important to reinvestigate the photoperiodical conditions required for the flowering of *Bryophyllum* and to elucidate the differences from earlier findings.

MATERIAL AND METHODS

Experiments on the flowering of *Bryophyllum daigremontianum* and *B. tubiflorum,* were carried out in the greenhouse of the University Botanical Garden. Plants were obtained from epiphyllous buds collected on plants grown in LD and, just after separation from the mother plants exposed to experimental photoperiodical conditions appropriate for the given experimental series. Under short day conditions plants were exposed to 8 hours of daylight (07.00-15.00 hours); from 15 p.m. till 7 a.m. the plants were shielded from light. Under long day conditions plants were exposed to 16 hours of light supplemented from 15 p.m. with light from fluorescent tubes of 2000-5000 lux of intensity, depending on their height. Moreover, on cloudy days, particularly in the autumn-winter period, both for the LD and SD conditions, daylight was supplemented with fluorescent light of the intensity mentioned above.

The temperature was registered on a weekly thermograph TZ-18. The monthly means of diurnal temperatures and the values of the sum of the products of the temperature times hours are given in Table 1.

Table 1

Mean monthly diurnal temperatures and temperature product in diurnal cycle* for the greenhouse of the Botanical Garden in Lublin in the period 1972-1976 and for Tananarive in Madagascar in the period 1933-1953 according to data of the "Meteorological Office"

Month	Lublin			Tananarive		
	Mean monthly diurnal temperatures		Temperature product in diurnal cycle*	Mean monthly diurnal temperatures		Temperature product in diurnal cycle*
	t_{max}	t_{min}		t_{max}	t_{min}	
I	25.0	17.5	510	26.1	16.1	506
II	25.5	18.0	522	25.6	16.1	500
III	27.9	16.8	536	26.1	15.6	500
IV	28.3	16.2	534	24.4	14.4	466
V	28.7	15.7	533	22.7	12.2	419
VI	28.3	14.0	508	20.6	10.0	367
VII	30.9	16.4	568	20.0	8.9	347
VIII	30.2	14.6	538	21.1	8.9	360
IX	25.5	14.3	478	23.3	10.6	407
X	23.8	16.0	478	26.7	12.2	466
XI	22.5	16.3	466	27.2	14.4	499
XII	22.9	16.2	469	26.7	15.6	508

* —calculated from the formula $\frac{t_{max}+t_{min}}{2} \times 24$

Gibberellic acid (GA_3 — "Fluka AG") was applied in the amount of 120-150 μg on the apical meristem of 6-month-old (*B. tubiflorum*) or 7-month-old (*B. daigremontianum*) plants.

Plants of *B. daigremontianum* and *B. tubiflorum* divided into 9 series of 7 plants each, were exposed to different photoperiodical conditions (the experiment were repeated 3 times):

1 — LD from the beginning to the end of the experiment;

2 — SD from the beginning to the end of the experiment;

3 — LD changed after 12 months to SD;

4 — LD changed after 6 months to SD;

5 — SD changed after 6 months to LD;

6 — photoperiod changed every two months starting with SD, (2 months SD, 2 months LD, 2 months SD etc.);

7 — natural photoperiodic conditions at Lublin latitude (51°N);

8 — photoperiod changed each 6 months starting with SD (simulating the natural rhythm of photoperiodic changes);

9 — SD + GA_3.

RESULTS

Results of experiments are given in Table 2.

The earliest flowering of *B. daigremontianum* was observed in the 1-st, 7-th and 9-th series. The best developed inflorescences (measured according to Penner, 1960) were observed in series 1. The flowering of plants from series 3, 5, 6 and 8 extended over a long time: some plants flowered after 15 months or even 12 months, whereas other plants in the same series flowered after 2-3 years. From Table 2 it can be seen that *B. daigremontianum* came into flower in those series in which mature plants were exposed temporarily or permanently to LD conditions (exposure to LD during the first 6 months of plant growth did not result in flowering: cf. series 4) and in the series 9 in which plants exposed to SD condition were treated with gibberelline. Flowering of *B. daigremontianum* in LD conditions was always observed in the winter (January, February). The formation of flowers in series 7 with "natural photoperiodic conditions" also occurred in the winter period, whereas in plants of LD-SD (series 3) in the summer (August) — in both series flowering occurred during exposure to SD. Confrontation of these observation with Table 1 leads to the supposition that the flowering of *B. daigremontianum* during LD exposure (series 1, 5, 6, 8) followed the period of decreased temperature and was evoked by it. The temperature products of the diurnal cycle were lowest in this period (September, December) and did not exceed the critical value estimated by Van de Pol (1972). In the case of plants flowering during SD exposure (series 3, 7) no correlation between flowering and temperature decrease was observed: plants in the series of "natural photoperiodic conditions" flowered at the same time as those of the LD series (it was a period preceded by low temperatures but at the same time a short day period) whereas the LD-SD series flowered at the time of highest diurnal temperatures (products of diurnal temperatures exceeded considerably the value of 500). Such high temperatures were also characteristic for the period preceding flowering.

Plants of the SD+GA_3 series flowered in various months (October, February). Flowering was always observed 1-2 months after treatment with gibberelline. Howeover, it is possible that the temperature played some role: in October the product of diurnal temperatures was rather low (close to the value of 472) and flowering in February was also preceded by a period of low temperatures.

The flowering of *B. tubiflorum* was observed only in four series: in the 3-rd, 7-th, 8-th and 9-th, but normally developed inflorescences observed only in series 7, 8 and 9, and only in these three series 100 per cent of plants flowered. The full flowering of *B. tubiflorum* was thus observed only in series 9 (plants in SD condition treated with gibbe-

Table 2

The flowering of *B. daigremontianum* and *B. tubiflorum* under different photoperiodic conditions (each series included 7 plants, the experiment was repeated 3 times)

No. and notation of series	*B. daigremontianum*				*B. tubiflorum*			
	Age of plants (in months)	Beginning of flowering	Percentage of flowering plants	Average stage of flowering according to Penner	Age of plants (in months)	Beginning of flowering	Percentage of flowering plants	Average stage of flowering according to Penner
1. LD	18-21	January	100	6	39		—	0
2. SD	43	—	—	0	39		—	0
3. 12 LD-SD	15-31	August	100	5	21	September	7.5	3-4
4. 6 LD-SD	43		—	0	39		—	0
5. 6 SD-LD	15-29	January	100	5	28		—	0
6. 2 SD-2 LD, ...	12-31	May	100	5	29		—	0
7. Natural photo-toperiodic conditions	18-21	January, February	100	5	18	December, January	100	5
8. 6 SD-6 LD...	21-32	February	100	5	20	September	100	5
9. SD+GA_3	9	October, February	100	5-6	7	November, January	100	5

relline) and in those series in which the photoperiod was changed severel times and the LD and SD duration were comparable with those occurring in nature (change of photoperiod each two months did not result in flowering: cf. series 6). It should also be noted, that flowering took place only during SD periods and no influence of temperature was observed.

DISCUSSION

Distinct differences observed in the photoperiodic reaction between *B. daigremontianum* and *B. tubiflorum*, both classified in the literature to the plant group of the same photoperiodic sensivity, as well as the differences from findings of other authors indicate that the photoperiodic requirements of these species cannot be comprised in a simple scheme.

According to the literature data, flowering of *B. daigremontianum* was observed, under the influence of successive treatment with long and then short day and also in SD conditions with gibberelline treatment.

However, the flowering of this species under conditions of constant LD or after trensferring it from SD to LD differs from the data of other authors. Previously only Resende (ref. Penner, 1960) obtained flowering in conditions of constant LD approximating the critical value.

It should also be stressed that our data agree with the findings of Van de Pol (1972) concerning the thermal requirements of *B. daigremontianum*. It seems however, that flowering can be induced just by a temperature decrease during LD, whereas according to Van de Pol it was indispensable as a factor acting jointly with short day or GA_3 induction. It is possible that the absence of flowering under conditions of constant LD in the experiments of other authors was caused by the constancy of mean temperature over the year.

The flowering of *B. tubiflorum* was observed in accordance with literature, only under LD followed by SD or on treatment with gibberelline under SD. After a single change of LD to SD flowering was observed only in 7% of plants, but in series 7 and 8 subjected to multiple changes of photoperiod (and in series 9 treated with GA_3) 100% of plants flowered.

Investigated both the species of *Bryophyllum* originate from Madagascar (Boiteau, Mannoni, 1949) where the photoperiod changes within a limited range (between 11 and 14 hours) whilst temperature differences are rather significant. During summer months (December--February) the sum of the products of temperature times hours exceeds 500 while during winter months (June-August) it falls below 400 [1]. The

[1] Tables of temperature, relative humidity and precipitation for the world. Part IV. London 1958.

flowering of both species of *Bryophyllum* on Madagascar takes place from June to August (I owe this information to Mr G. Cremers from the ORSTOM Institute in Tananarive), thus it occurs during the period of shortened days and markedly lowered temperature. In the period preceding flowering diurnal products, starting from April, were also below the value of 472. Taking this into account together with the results of experiments presented above, it can be concluded that in the flowering of *B. daigremontianum* a double control was probably evolved depending on a reaction equally sensitive to the shortening of the day as to the lowering of temperature. One of these two factors would be sufficient for the initiation of flowering. In the case of *B. tubiflorum* the initiation of flowering seems to be a response to more than two subsequent periods of shortening of the daylength: lowering of temperature favours the initiation or perhaps is even necessary but is not sufficient.

The phenomenon of interaction of photoperiod and temperature influences during the initiation of flowering or even the phenomenon of mutual replacement of these factors suggested above on *B. daigremontianum* is not an exception. Schwwemmle (1957) suggested that high temperature may be a physiological equivalent of a period of darkness and low temperature an equivalent of a period of light. Lang (1965) reported on SLD plants (also requiring two different photoperiods) that the first part of floral induction may be accomplished by treating the plants with low temperatures or alternatively by treating them with SD. Many similar examples were provided also from investigations on SD plants (cf. Van de Vooren, 1971; Heide, 1977; Deronne, Blandon, 1977). In the SLD plant group a separate subgroup is distinguished, consisting of plants in which low temperature can substitute short-day action, so that at low temperatures the plants behave as LD ones (Vince-Prue, 1975). It is probable that among long-short-day plants such groups could also be distinguished, and *B. daigremontianum* should be included into it.

This paper suggests the possibility of replacing the short-day part of floral induction of *Bryophyllum daigremontianum* by lowering of the temperature. To confirm this suggestion, experiments carried out under conditions of regulated temperature are necessary.

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Warunki fotoperiodyczne i termiczne doprowadzające do kwitnienia Bryophyllum daigremontianum (Hamet. et Perr.) Berg. i Bryophyllum tubiflorum Harv.

Streszczenie

Stwierdzono wyraźne różnice w reakcji fotoperiodycznej między dwoma gatunkami *Bryophyllum*, zaliczanymi w literaturze do roślin długiego-krótkiego dnia. Kwitnienie *B. daigremontianum* obserwowano w kilku układach fotoperiodycznych

m. in. przy stałej ekspozycji w DD lub przy przeniesieniu z KD do DD tzn. w układach uznanych w literaturze za nieindukujące. Wydaje się, że warunkiem kwitnienia *B. daigremontianum* jest wystarczająco długa ekspozycja w DD a następnie działanie jednego z dwu czynników: skrócenie dnia lub obniżenie temperatury. Odpowiedź kwitnieniową *B. tubiflorum* uzyskiwano w bardziej specyficznych i nielicznych układach fotoperiodycznych. Wydaje się, że warunkiem kwitnienia tego gatunku jest kilkakrotna zmiana fotoperiodu.