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SOME EXPERIMENTS ON GROWTH, REPRODUCTIVE DEVELOPMENT AND PRODUCTIVITY¹

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Let me first of all express my deep sense of gratitude to the Indian Botanical Society for electing me for the award of Birbal Sahni Medal for the year 1977. This is indeed a great honour that a botanist can feel proud of, particularly as the Medal has been instituted after the name of the great world renowned botanist Birbal Sahni. I, of course, feel that the credit to get this award actually goes to the colleagues and students who have worked with me from time to time during the period of 36 years that has elapsed since my induction to research in plant physiology under the guidance of the late Professor R. S. Chaudhri in the Banaras Hindu University at Varanasi.

Today I propose to share with you, ladies and gentlemen, some of the results that we have obtained in our experiments on growth, reproductive development and productivity. I have selected this topic firstly because it is customary on such occasions to talk about the work one is engaged in and secondly because the

topic is of great agricultural importance. This work was started at the Indian Agricultural Research Institute, New Delhi under the guidance of my revered guru, Professor J.J. Chinoy who may rightly be considered at present as the father of modern plant physiology in this country. It is a happy coincidence that he happens to be in our midst this afternoon and further that the Medal is to be presented to me by Professor S.M. Sircar, who is the topmost plant physiologist of the country and is the General President of this session of the Indian Science Congress.

Extensive studies on 260 varieties of wheat carried out since 1941 have demonstrated that the length of the vegetative period of a variety determines not only the rate and magnitude of different components of growth but also the metabolic drifts of nutritional and regulatory substances. These studies on relationships between growth and development were later extended to a number of other plants. Thus, six different types of millets were grown at 32-days intervals throughout the year. The growth pattern of three of these—*Panicum miliaceum*, *Setaria italica* and *Eleusine coracana*—in

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different sowings is shown in figures 1-3 and the morphology of ears produced on these and on *Echinochloa frumentacia* in figures 4-7, respectively. Marked differences in the growth pattern of plants and the morphology of ears were observed with an alteration in environmental complex due to change in the time of sowing. The pattern of development of lateral buds varied in plants of different sowings. Thus, in early sowings the development of lateral buds was confined to the lower part of the plant, occurred prior to flowering of the main shoot and was in acropetal order. On the other hand in later sowings, lateral buds elongated only after the emergence of ears on the main shoots and occurred in basipetal order from top downwards. It is as a consequence of this that the growth pattern varied markedly in plants of different sowings

(Nanda et al. 1957 a, b, c and Nanda 1964). Figure 8 demonstrates that the ears of these four millets which differ so markedly in one sowing (first row) resemble one another more closely (third

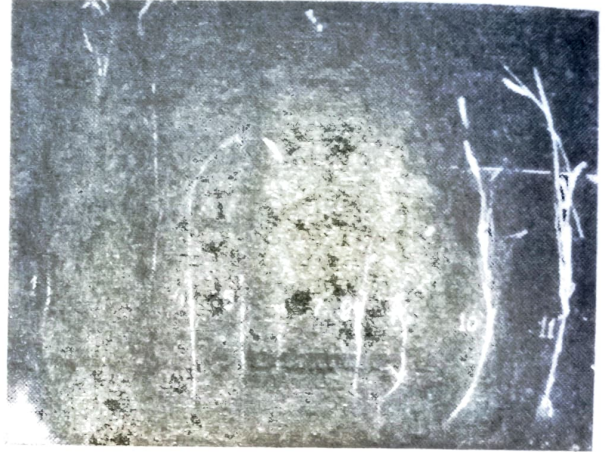


Fig. 2



Fig. 3

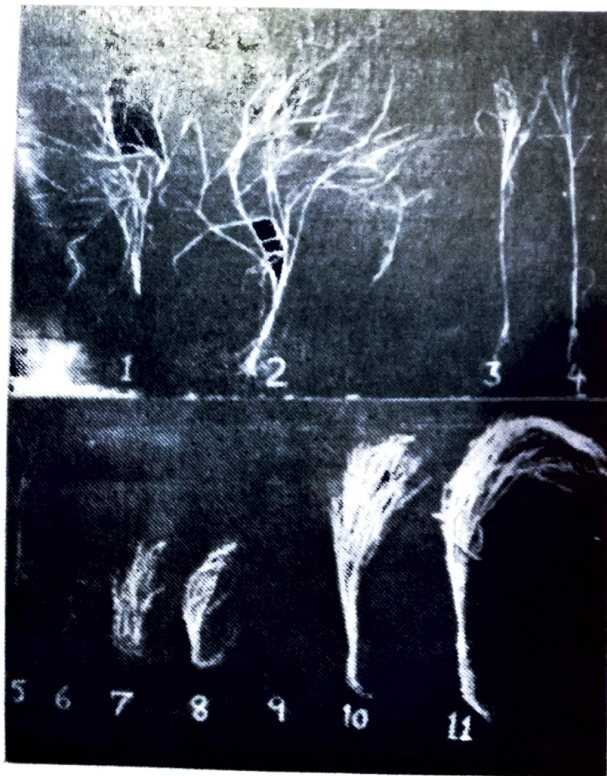


FIG. 1. Growth pattern of *Panicum miliaceum* in different sowings made at 32-day intervals throughout the year. First sowing was done in the month of April in Delhi. Data from Nanda (1947, 1964).

FIGS. 2-3. Growth patterns of *Setaria italica* (Fig. 2) and *Eleusine coracana* (Fig. 3) in different sowings made at 32-day intervals throughout the year. First sowing was done in the month of April in Delhi. Data from Nanda (1957).

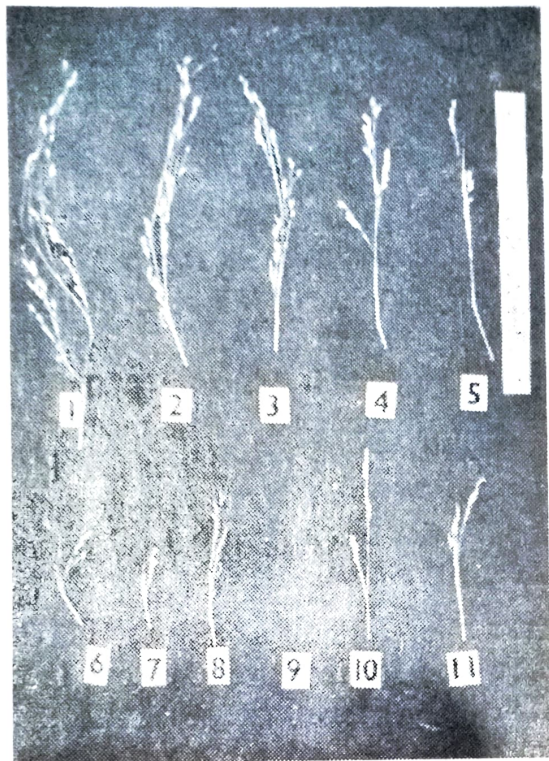


Fig. 4



Fig. 5

FIGS. 4-5. Ears of *Panicum miliaceum* (Fig. 4) and *Setaria italica* (Fig. 5) in different sowings made at 32-day intervals throughout the year. First sowing was done in the month of April in Delhi. Data from Nanda (1957, 1964).

row) than each resembles its own type in other sowings.

That the emergence of lateral branches and their flowering is correlated with the flowering of the main shoot is clearly brought out from another experiment in which *Panicum miliaceum* was sown

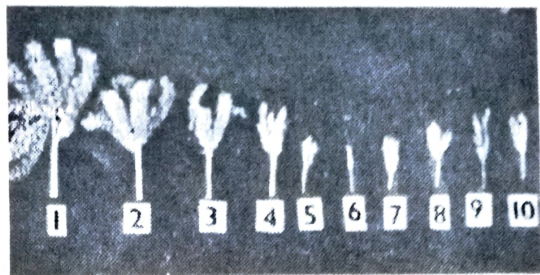


FIG. 6. Ears of *Eleusine coracana* in different sowings made at 32-day intervals throughout the year. First sowing was done in the month of April in Delhi. Data from Nanda (1957, 1964).

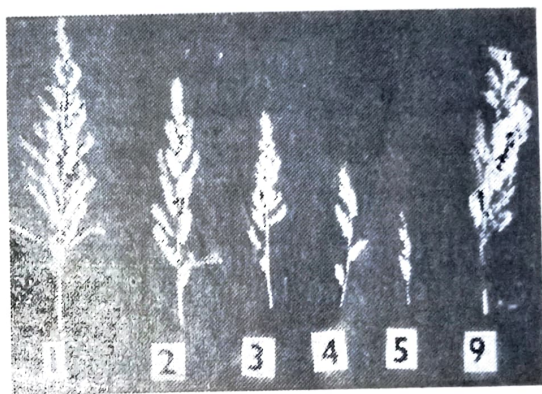


FIG. 7. Ears of *Echinochloa frumentacia* in different sowings made at 32-day intervals throughout the year. First sowing was done in the month of April in Delhi. Data from Nanda (1957).

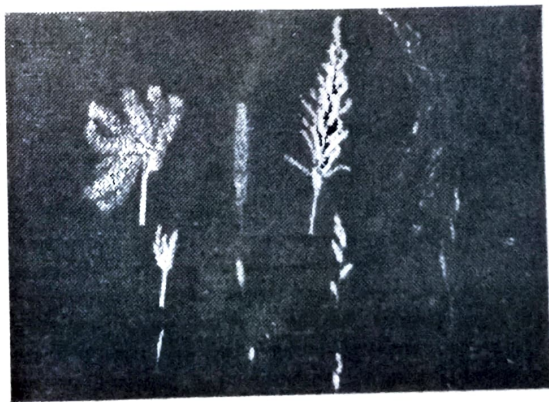


FIG. 8. Ears of four different types of millets i.e., *Eleusine coracana*, *Setaria italica*, *Echinochloa frumentacia* and *Panicum miliaceum* in three different sowings.

and the plants obtained were subjected to varying photoperiods. The results are

shown in figure 9. Plants exposed to long day condition (LD) did not flower at all. Branches emerged one after the other in acropetal succession. But in plants exposed to normal day (ND) and short day (SD) conditions, the development of branches took place in basipetal succession and occurred after the emergence of the ears on the main shoots. The emergence of secondary and tertiary branches and their flowering also followed the same pattern as the primary branches (Nanda, 1958). Similar relationship of branching pattern with flowering was observed in other plants including some forest plants (Nanda and Chinoy 1958 Nanda 1961, 1962 a and b). In *Crotalaria juncea* (Nanda 1962 a), the branches remained very small and arose in basipetal order during the time of the year when the environmental conditions

were inductive but elongated 4-5 times the length of the main shoot with complete arrestment of lateral buds during the non-inductive photoperiods (Fig. 10).

In *Anchusia officinalis* (Fig. 11) the development of lateral buds was acropetal earlier in growth, then stopped till the flowering of the main shoot and became basipetal after that (Nanda 1964). Both the acropetal and basipetal patterns of branch emergence were, therefore, observed on the same plant. Considerable evidence has, thus, accumulated to show that the qualitative changes in the growing apex from vegetative to reproductive state exert a marked influence on the development of axillary meristems below it and on the emergence of branches produced from them.

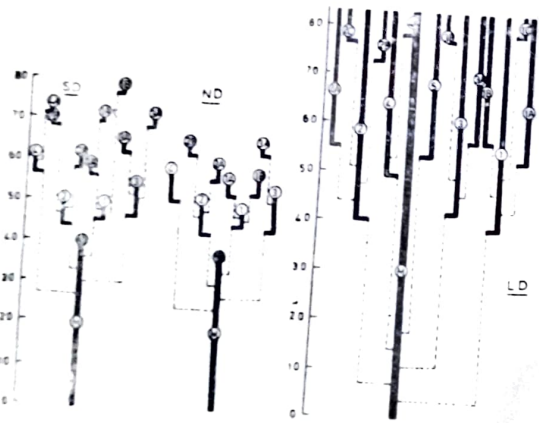


FIG. 9. Diagrammatic representation of SD, ND and LD plants showing the vegetative periods of the main shoot and branches of different orders in *Panicum miliaceum*. The vertical columns represent the vegetative periods and the circles terminating these columns represent the inflorescence. The absence of circles at the end of vertical columns, as in LD plants, indicates lack of flowering. The numbers within circles represent the order of emergence of branches and the position of the node on the plant is indicated by an arrow that terminates below a dotted line which connects it with the main shoot in the case of primary branches and a primary branch in the case of secondary branches. Data from Nanda (1964, 1958).

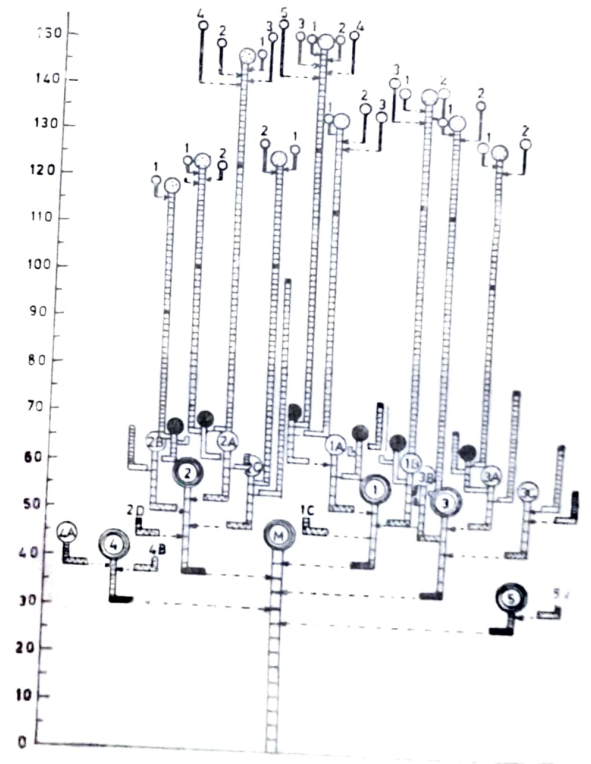


FIG. 10. Diagrammatic representation of a plant of *Crotalaria juncea* showing the number of branches and nodes as well as the height attained by the main shoot and branches of different orders. The vertical columns in this figure represent the height of the main shoot and the branches in cm. Data from Nanda (1962).

All the plants that were selected for investigation till then, however, belong to the type in which the growing apex terminates in an inflorescence. We were thus, on a look out for a plant in which the apical growing point should continue meristematic activity without itself changing into reproductive state. It was under these circumstances that our choice fell on *Impatiens balsamina* L., which is an ornamental plant belonging to the family Balsaminaceae. As the apical growing point in *Impatiens balsamina* itself does not undergo any qualitative change, it was expected that the development of lateral buds will always be acropetal and never basipetal. And that is exactly what happened (Nanda and Kumar 1966). The lateral buds in this plant developed one after the other in acropetal succession. When placed under inductive conditions these buds became floral (Fig. 12), while on the other hand, under non-inductive conditions these developed into vegetative branches (Fig. 13). Whether floral or vegetative, these buds never developed in basipetal order. These results demon-

strate that some physio-chemical changes which cause the transformation of the growing apex from vegetative to the reproductive state are of paramount importance in determining the behaviour of lateral buds and consequently the growth pattern of the plant.

Although rediscovered for a different purpose in 1959, the extensive use of this plant in probing the fascinating mystery of floral morphogenesis was started in 1963 in the Panjab University at Chandigarh. The choice was based on

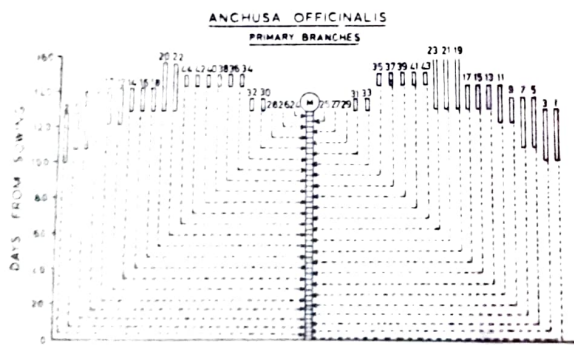


FIG. 11. Diagrammatic representation of a plant of *Anchusa officinalis* showing the number of primary branches as well as the lengths of the vegetative periods of the main shoots and branches. The vertical columns in this figure represent the vegetative periods. The order of emergence of branches is shown by the numbers shown within circles which represent the inflorescence in each case. The absence of circles at the end of certain columns indicates that these did not flower at all. Data from Nanda (1966).

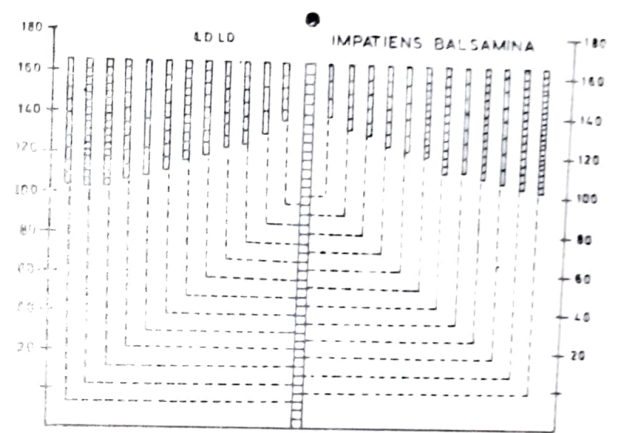


Fig. 12

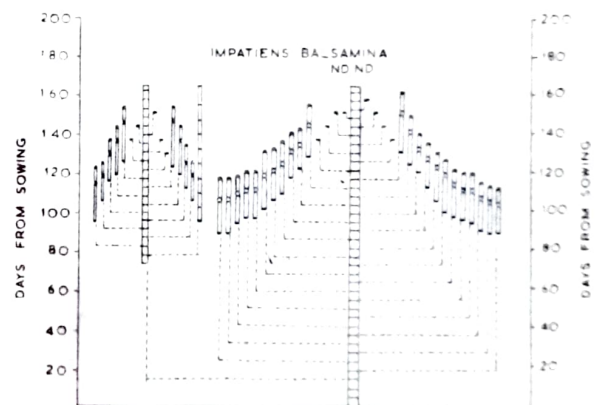


Fig. 13

FIG. 12-13. Diagrammatic representation of plants of *Impatiens balsamina* under SD (Fig. 12) and LD (Fig. 13) conditions showing the conversion of axillary meristems into floral buds under SD conditions and into vegetative branches under LD conditions. In both cases the order of emergence is acropetal. The apical meristem does not change from vegetative to reproductive state i.e., the plant is indeterminate. Data from Nanda (1966).

simple habit of the plant, its short span of life and indeterminate nature. The plant has now established itself as a unique physio-morphogenetic system. The spectacular results that have since accumulated have opened up a new era in the history of research on growth and reproductive development.

Some of the significant findings that have since emerged are presented here :

2 or 3 short days required for floral bud initiation.—*Impatiens balsamina* is a qualitative short day (SD) plant (Nanda and Krishnamoorthy, 1967 and Nanda et al. 1965) which requires 3 SD cycles for the initiation of floral buds and at least 8 for them to develop into flowers. However, even 2 SD cycles were found to cause floral induction in later experiments probably due to more favourable prevailing temperatures (Sawhney et al. 1972) Plants continued to grow vegetatively under continuous illumination (Fig. 14) appearing like a miniature tree after one year of growth.

The critical dark period for the initiation



FIG. 14. Effect of photoperiod on *Impatiens balsamina*. LDLD plants were sown under long day condition and were left there throughout the growing period. These remained vegetative and produced lateral branches in acropetal succession. NDSD plants were sown under normal day but were transferred to short day later. Lateral buds produced were reproductive. Data from Nanda and Kumar (1966).

of floral buds in this plant is $8\frac{1}{2}$ hr alternating with $15\frac{1}{2}$ hr light at $26\pm 1^\circ\text{C}$ (Nanda, 1962), although the daily dark requirement for floral bud initiation decreased to 8 hr at lower temperatures prevailing in March (Sharma 1976). The critical photoperiod, thus, changes with the prevailing temperature conditions.

Floral buds revert to vegetative growth under non-inductive photoperiods.—The plant requires short day cycles not only for the initiation of floral buds but also for them to develop into flowers. The induced floral buds revert to vegetative growth if the SD cycles received by them fall short of the number which is required for their opening into flowers and interestingly this occurs even after the formation of ovules and anthers (Fig 15).

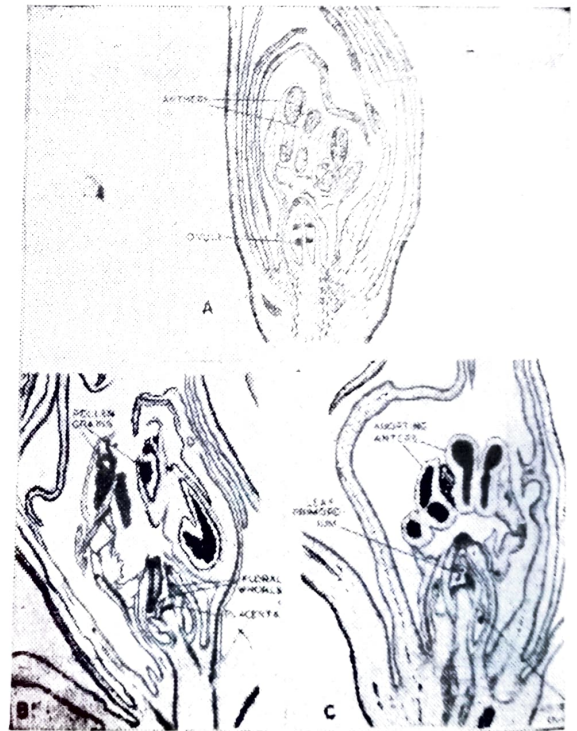


FIG. 15. Photomicrographs of median longitudinal sections of floral buds at different stages of development of *Impatiens balsamina*. Note the normal development of floral appendages and essential organs under continuous SDs (a) and the termination of mature anthers with pollen grains and placenta inside the ovary into a vegetative apex after the formation of ovular primordia (B) and abortive ovules (C).

As far as we are aware, this is perhaps the only report where reversion of floral buds has been shown to occur even after such an advanced stage in the development of flowers. In this connection it is to be noted that while in plants receiving 4 SD cycles all the initiated floral buds revert, in those receiving more than 8 SD cycles it is only the upper younger ones that revert while the lower ones open into flowers (Table I). The reversion of

TABLE I

MAGNITUDE OF FLOWERING AND TIME OF FLORAL BUD REVERSION IN PLANTS EXPOSED TO VARYING NUMBERS OF SHORT DAY CYCLES.

Treatment	No. of floral buds	No. of flowers	Days to reversion
Continuous LD	—	—	—
4 SD	4.6	—	3-10*
16 SD	11.0	6.0	8-25*
32 SD	16.1	9.5	15-50*
Continuous SD	22.4	13.5	—

*The first figures indicates the days to reversion of the uppermost, the second of the lowermost floral bud.

Data from Krishnamoorthy and Nanda (1968).

upper floral buds occurs even in plants that have received as many as 90 SD cycles demonstrating thereby that in this plant the floral stimulus does not self-perpetuate as is known to happen in other plants. It would, thus, appear that SD stimulus is required even for the completion of gametogenesis as the development of anthers and ovules is arrested and the tip of placenta starts producing leaf primordia instead of floral appendages when plants are transferred

to non-inductive photoperiods (Krishna moorthy and Nanda, 1968).

Apical growing point can be made to flower.—The plant is indeterminate in nature. It was considered rather intriguing that the terminal meristem should remain vegetative, while the axillary meristems in close proximity to it become floral under inductive photoperiods. In order to check if it was due to exhaustion of floral stimulus, a surgical experiment was designed. The axillary floral buds in a group of plants maintained under inductive photoperiods were surgically removed as soon as they could be made out, thereby preventing the utilization of floral stimulus on the way and enabling it to reach the apical meristem. It was observed that this treatment caused a considerable increase in the size and pigmentation of leaves as well as in the size and number of petiolar glands. The younger leaves at the top of debudded plants, after some time started crowding up, the apices got swollen up and ultimately developed into visible flower buds (Fig. 16). The plant, thus became determinate. In contrast to this the apices in control plants continued to



FIG. 16. Two plants of *Impatiens balsamina* maintained under inductive photoperiods. On the left is a normal plant with axillary fruits and flowers but vegetative apex. Leaves on the lower nodes have abscised. On the right is a debudded plant which shows large thick leaves and a terminal floral bud.

grow producing axillary floral buds in acropetal succession (Nanda & Purohit 1967).

Short day effect is summated through intercalated LD cycles.—Another interesting point that has emerged from these investigations is that the effect of individual SD cycles which in themselves are not inductive, can be summated even when intercalated by as many as 16 LD cycles. This means that in this plant the sub-threshold stimulus of inductive SD cycles can persist through long non-inductive periods and is not destroyed (Krishnamoorthy and Nanda, 1967). This is in marked contrast to other long

and short day plants where fractional induction has been reported only when the number of non inductive intercalated cycles is small enough to permit sub-threshold inductive effect to persist (Fig. 17).

In fact intercalated non-inductive cycles hasten both the initiation as well as development of floral buds and the hastening effect increases with an increase in the number of intercalated long days (Toky and Nanda, 1969). Thus, in some experiments plants were exposed to 4, 8 or 12 SD cycles either consecutively or individually separated by 4-8 LD cycles. The results presented in tables II and

TABLE II
EFFECT OF INTERCALATED LDS ON FLOWERING OF PLANTS
RECEIVING A TOTAL OF 4 AND 8 SD CYCLES.

Treatment SD+LD= total SD cycles	Days to floral bud initiation from the first day of treatment (from the day of completion of 4 SD cycles)	Days of flowering from the first day of treatment (from the day of completion of 8 SD cycles)	Number of intercalated LDs received till completion of 4 (8) SD cycles	Mean number of floral buds (flowers)	Plants flowering out of 10
4+0=4	8.0(4.0)	(—)	0(0)	14.5(—)	0
1+1=4	9.0(2.0)	59.0(52.0)	3(—)	12.0(1.0)	1
1+2=4	11.7(1.7)	54.0(44.0)	6(—)	13.0(1.5)	2
1+4=4	17.0(1.0)	50.0(34.0)	12(—)	12.5(2.0)	4
2+1=4	9.4(4.4)	47.0(42.0)	1(—)	11.5(3.0)	1
2+2=4	9.4(3.4)	44.0(38.0)	2(—)	15.5(2.5)	4
2+4=4	12.9(4.9)	(—)	4(—)	13.0(—)	—
8+0=8	9.3(5.3)	26.0(18.0)	0(0)	15.0(7.8)	—
1+1=8	11.6(4.6)	33.0(18.0)	3(7)	13.3(2.6)	—
1+2=8	12.6(2.0)	31.7(9.7)	6(14)	10.7(5.6)	—
1+4=8	14.1(1.9)	37.0(1.0)	12(28)	14.0(4.5)	—
2+1=8	11.0(6.0)	35.8(24.8)	1(3)	13.4(3.8)	—
2+2=8	9.3(3.3)	32.4(18.4)	2(6)	14.5(6.0)	—
2+4=8	11.3(3.3)	32.4(12.4)	4(12)	15.0(6.2)	—
4+1=8	8.2(4.2)	37.0(18.0)	0(1)	14.0(5.1)	8
4+2=8	8.3(4.3)	31.0(21.0)	0(2)	14.0(4.0)	8
4+4=8	7.8(3.8)	28.5(16.5)	0(4)	14.7(6.3)	9
C-SD=60	8.8(4.3)	28.4(20.4)	0(0)	11.0(7.3)	10
C-LD=0	(—)	(—)	(—)	(—)	—

Data from Toky and Nanda, (1969).

INTERCALATION EXPERIMENT

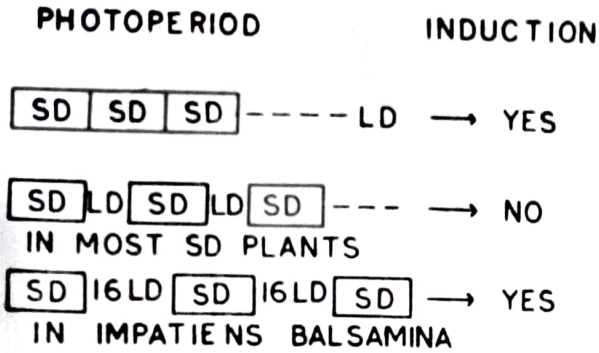


FIG. 17. Effect of individual SD cycles intercalated by long days (LDs) on the flowering of *Impatiens balsamina* and other short day plants. While most short day plants fail to flower when SD cycles are intercalated by LDs, it is not so in *Impatiens balsamina*.

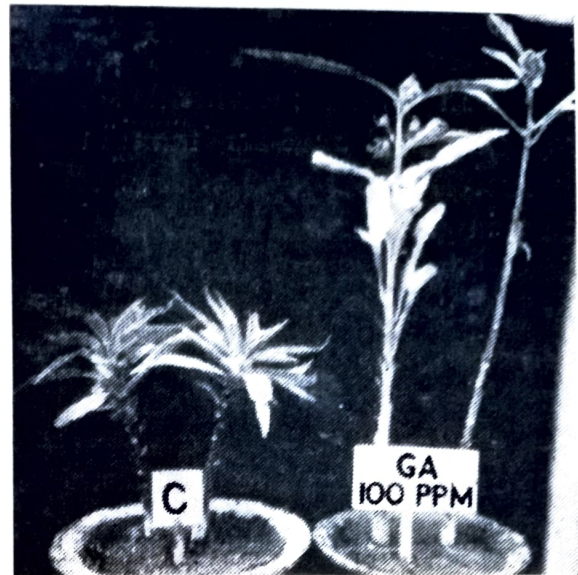


FIG. 20. *Impatiens balsamina* L. treated with GA₃ under continuous illumination (right) and control (left). Flowers can be seen on the treated plants.

INTERRUPTION EXPERIMENTS

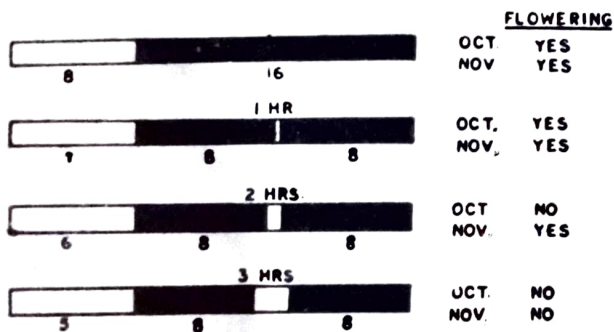


FIG. 18. Effect of light interruption given in the middle of dark period in October and November in flowering of *Impatiens balsamina*. Floral buds are formed even when the dark period is interrupted by light for 2 hr.

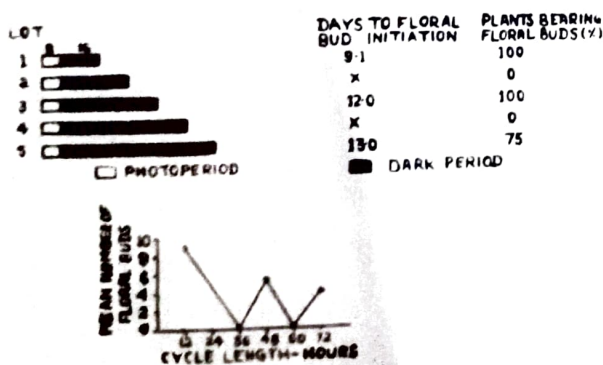


FIG. 19. Effect of cycles of varying lengths with 8 hr of light alternating with varying durations of dark on flowering of *Impatiens balsamina*. Floral buds are produced on plants subjected to 24, 48 or 72 hr cycles but not on those subjected to 36 or 60 hr cycles.

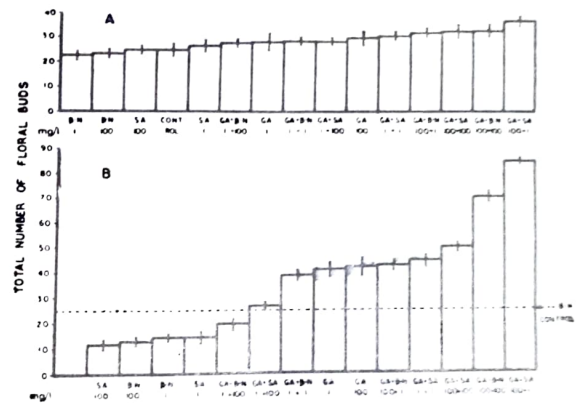


FIG. 21. Effect of GA₃, SA and B-N on days to floral bud initiation. Vertical bars represent 95% level of confidence. A: 8-hr photoperiod. B: 24-hr photoperiod.

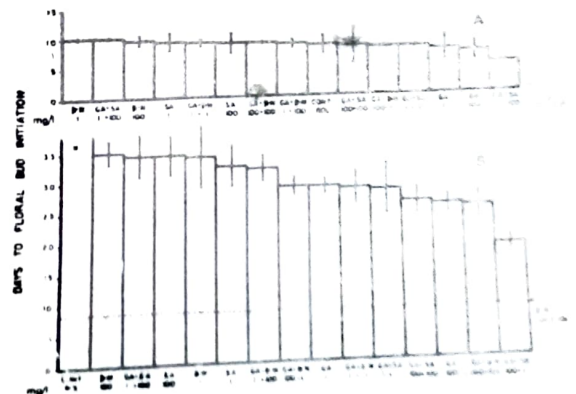


FIG. 22. Effect of GA₃, SA and B-N on the number of floral buds produced after 45 days on the main axis of each plant. Vertical bars represent 95% level of confidence. A: 8-hr photoperiod. B: 24-hr photoperiod.

Table III show that floral buds after the completion of 8 SD cycles initiated earlier in plants in which individual SD cycles were intercalated by LDs than in those which received SD cycles consecutively. In fact, in plants receiving individual SD cycles intercalated by 4 LDs, floral buds were initiated even before the completion of 4 SD cycles (Table II). With the intercalation of SD cycles by LDs, even the number of SD cycles required for the development of floral buds into flowers was reduced from 8 to 4 in such plants. It would, thus, appear that non-inductive photoperiods intercalated between inductive cycles tend to stabilize the floral stimulus.

Light interruption of dark period.—An interruption of the dark in the middle even for a few minutes in qualitative short

day plants in known to completely inhibit the induction of floral buds, demonstrating the significance of uninterrupted dark period. However, this plant behaves in a different manner. An interruption of the dark period in the middle by light even for 2-3 hr does not inhibit flowering although delays it (Nanda et al. 1969). The results are presented diagrammatically in figure 18.

Plant exhibits endogenous rhythm in flowering response to photoperiod.—From another experiment in which the light period was maintained at 8 hr but the dark period was varied from 16-64 hr, it is found that flowering occurs in plants receiving 24, 48 and 72 hr cycles and not at all in those receiving 36 and 60 hr cycles (Nanda et al. 1969) indicating thereby the operation of rhythmical process with a periodicity of 24 hr in flowering response of this plant to photoperiod (Fig. 19).

Inductive requirement can be partially substituted by non-inductive photoperiods. Another significant point that has emerged from investigations on this plant is that a part of the photoinductive requirement can be met even by long days (LDs) provided they have 4 or more hr of darkness in each cycle (Sawhney et al. 1972). It appears that the floral stimulus generated during darkness is additive regardless of whether the dark period forms a part of the inductive or non-inductive cycles provided, of course, a certain critical dark period has already been received by the plant. Thus, of the two SD cycles which are required for the initiation of floral buds in this plant, it is the first cycle which is obligatory but the second one can be substituted even by non-inductive LD cycles with 4 or more hr of darkness in each cycle (Table IV). This, perhaps, is the only available report

TABLE III

EFFECT OF INTERCALATED LDs ON FLOWERING OF PLANTS RECEIVING A TOTAL OF 12 SD CYCLES.

Treatment SD+LD= total SD cycles	Days to floral bud initiation from the first day of treat- ment (from the day of completion of 4 SD cycles)	Days to flowering from the first day of treatment (from the day of completion of 8 SD cycles)
12+0=12	10.0(6.0)	40.0(32.0)
1+1=12	10.0(3.0)	51.0(36.7)
1+2=12	11.1(1.0)	56.6(34.6)
1+4=12	15.1(-1.0)	59.0(23.0)
4+1=12	9.0(5.0)	41.8(32.8)
4+2=12	10.0(6.0)	42.8(32.8)
4+4=12	10.0(6.0)	40.0(28.0)
4+8=12	9.0(5.0)	45.8(37.0)

Data from Toky and Nanda (1969).

TABLE IV

EFFECTS OF SUPPLEMENTARY LONG DAYS WITH VARYING DARK PERIODS ON INDUCTION AND NUMBER OF FLORAL BUDS IN *IMPATIENS BALSAMINA*

Losses	Pre-treatment	Post-treatment			Days to floral bud initiation	First node to initiate floral buds	Mean number of floral buds
	Number of SDs with light period of	Number of LDs with light period of					
		8 hr	24 hr	20 hr			
1	0	20	0	0	—	—	0
2	1	20	0	0	—	—	0
	1	0	20	0	23.0±0.42	34.4±1.0	4.0±0.02
	1	0	0	20	20.5±0.35	25.9±0.43	5.0±0.01
3	2	20	0	0	14.4±0.21	26.4±0.39	9.2±0.12
	2	0	20	0	11.0±0.28	26.1±0.44	11.2±0.12
	2	0	0	20	11.0±0.30	25.6±0.28	12.0±0.12
4	3	20	0	0	8.0±0.25	25.8±0.35	11.4±0.10
	3	0	20	0	8.0±0.15	26.3±0.56	14.5±0.21
	3	0	0	20	8.0±0.20	26.2±0.47	14.6±0.12

of the partial substitution of inductive requirement by non-inductive photoperiods and should set us rethinking on reversing our concept of critical photo-inductive requirement.

Gibberellins can substitute for the photo-inductive requirement.—One of the spectacular responses of this qualitative short day plant is that GA₃ is able to cause induction of floral buds under strictly non-inductive photoperiods (Nanda et al. 1967, 1968, 1969, 1977) (Fig. 20). Table V shows that GA₄₊₇, GA₁₃ and even (—)—kaurene, which is considered to be a precursor of gibberellin biosynthesis, can also effectively cause floral induction in this plant (Nanda et al. 1969). This finding is not in accord with the 'gibberellin-anthesin' concept of flowering put forth by Chailakhyan which is based upon the assumption that short day plants under long day conditions are

deficient in anthesins but not in gibberellins and that anthesins can be formed in these plants only under short days. More recently it has been shown that *Impatiens balsamina* is not the only short day plant in which gibberellins induce floral buds under non-inductive photoperiods. They are able to induce flowering in a number of other short day plants (Nanda et al. 1977; Datta et al. 1976; Kumar et al. 1977; Datta and Nanda 1978). Table VI shows that GA₃ induces flowering in the qualitative short day plants *Panicum miliaceum* and *Panicum miliare* and hastens it in the quantitative short day plant *Setaria italica* under non-inductive long days. GA₃ is reported to cause floral induction under non-inductive photoperiods in *Zinnia elegans* (Sawhney and Sawhney 1976), *Dahlia palmata* (Kumar et al. 1977) and *Chrysanthemum morifolium* (Pharis, 1972) as well.

TABLE V

EFFECT OF EXOGENOUS APPLICATION OF GIBBERELLINS ON FLOWERING UNDER INDUCTIVE AND NON-INDUCTIVE PHOTOPERIODS.

Treatment (100 mg/l)	Photo-period	Days to floral induction	Mean number of floral buds	Percent plants induced
Control		13.1	20.4	100
GA ₃		12.2	16.4	100
GA ₁₃	8	14.8	18.1	100
GA ₄₊₇		13.3	18.00	100
(-)-kaurene		15.7	15.2	100
Control		—	—	0
GA ₃		59.0	23.5	100
GA ₁₃	24	81.9	16.5	67.5
GA ₄₊₇		49.0	20.1	100
(-)-kaurene		88.0	8.9	75

Data from Nanda et al., (1969)

TABLE VI

EFFECT OF GIBBERELIC ACID (100 MG/l) ON DAYS TO EAR EMERGENCE IN *PANICUM MILIACEUM*, *PANICUM MILIARE* AND *SETARIA ITALICA* UNDER 8 AND 24-H PHOTOPERIODS.

Species	Photoperiod	Control	GA ₃ (100 mg/l)
<i>Panicum miliaceum</i>	8-h	34.4±1.80	33.6±2.10
<i>Panicum miliaceum</i>	24-h	0	44.4±2.40*
<i>Panicum miliare</i>	8-h	34.0±0.00	32.5±0.43
<i>Panicum miliare</i>	24-h	0	72.7±0.25*
<i>Setaria italica</i>	8-h	29.7±0.35	17.9±1.00
<i>Setaria italica</i>	24-h	53.7±2.80	40.5±1.40

*Ears short, with a small number of spikelets, spikelets sterile.

Apart from their effect on flowering, gibberellins affect vegetative growth of

this plant as of other plants although the effect varies with the gibberellin. Thus, while GA₃ and GA₄₊₇ promote extension growth significantly, GA₁₃ and (-)-kaurene do not affect it. Effects on extension, growth and flowering, thus, appear to be mediated through processes which act independent of each other (Sawhney et al. 1970; Sawhney et al. 1970; Sawhney et al. 1972).

Sub threshold GA₃ effect can be summated to the sub-threshold photoinductive effect.—Another interesting point that has emerged from these investigations is that the effect of sub-threshold doses of gibberellins can be effectively summated to the effect of sub-threshold photoinductive cycles and this occurs even when the two are intercalated by as many as 16 long days (Table VII). In fact, floral bud initiation is actually hastened further supporting the assumption that intercalated long days act to stabilize the stimulus (Nanda et al. 1975, Nanda and Jindal, 1976). These results are similar to the summation effect of individual SD cycles described in previous section and are suggestive that the processes involved in photo- and GA₃-caused induction are similar.

Phenolic compounds can also substitute for the photoinductive requirement.—Phenolic compounds have been regarded as analogues of growth regulators involved in the regulation of physiological phenomena. It is rather interesting that monophenols salicylic acid and β-naphthol (Nanda et al. 1976), diphenols, caffeic acid, dihydroxy-phenylalanine (DOPA) and resorcinol and polyphenols chlorogenic and tannic acids (Nanda and Kumar, 1977) all induce floral buds in this plant under strictly non-inductive photoperiods. More interesting is the fact that they synergise the effect of GA₃ in hastening

TABLE VII

EFFECT OF INTERCALATED LONG DAYS BETWEEN 1 SD CYCLE AND GA₃ APPLICATION ON FLOWERING OF *IMPATIENS BALSAMINA*

Treatment	Days to floral bud initiation	First node to initiate floral buds	Mean number of floral buds	Number of plants with floral buds out of 8
1 SD-LD	—	—	—	—
1 SD-4 LD-GA ₃	8.2	17.4	7.3	8
1 SD-8 LD-GA ₃	10.3	19.4	6.9	7
1 SD-12 LD-GA ₃	14.8	19.1	5.1	7
1 SD-16 LD-GA ₃	18.4	20.0	3.6	5
LD-W	—	—	—	—
LD-GA ₃	20.8	22.7	3.7	4

floral bud initiation and also in the formation of floral buds and flowers (Table VIII and Figs. 21-23). This is of particular significance as tannins are known to be GA₃ antagonists. These results are of great significance in maximization of yield. This is evident from the fact that they stimulate stem elongation, increase the number of branches and ears, enhance grain weight and increase grain yield in millets like *Panicum miliaceum* (Figs. 24 and 33) and *Setaria italica* (Fig. 25) (Nanda et al 1977, Datta et al. 1976) and also in Triticale (Fig. 26) (Datta and Nanda, 1978).

Purine derivatives also substitute for photoinductive requirement.—More recent work has shown that purine derivatives 3', 5'- and cyclic AMPs and GMPs can also be added to the list of chemicals which are able to induce floral buds in this plant under non-inductive photoperiods (Nanda et al. 1976). This is signifi-

TABLE VIII

EFFECT OF GIBBERELLIC ACID AND PHENOLS EACH ALONE AND IN COMBINATION ON FLOWERING UNDER INDUCTIVE AND NON-INDUCTIVE PHOTOPERIODS.

Treatment (100 mg/l)	Photo-period (h)	Days to floral induction	Mean number of floral buds	Percent plants induced
Control		8.0	35.6	100
Tannic acid	8	8.6	36.8	100
Chlorogenic acid		7.3	37.6	100
Control		—	—	0
Tannic acid	24	27.5	51.0	100
Chlorogenic acid		22.8	49.6	100
Control		9.2	34.0	100
Caffeic acid	8	6.9	39.0	100
Cathechol		8.6	36.6	100
Control		—	—	0
Caffeic acid	24	38.0	32.0	100
Cathechol		—	—	0
Control		8.0	25	
B-naphthol	8	9.0	23	
Salicylic acid		8.2	25	
Control		—		
B-naphthol	24	35		
Salicylic acid		34		

Data from Nanda et al., (1976)

cant as cyclic AMP is considered to induce gibberellin biosynthesis at genomic level and may as such mediate this effect on flowering. But induction is caused even by 3'— and 5'—, AMPs and GMPs although the inductive effect of cyclic purine derivatives manifests itself much earlier than that of non cyclic purine derivatives (Table IX). It is yet to be investigated if the mechanism of action

of all these purine derivatives is similar or different particularly as cyclic GMP is known to antagonise the affect of cyclic AMP in growth processes.

Auxins delay while triiodobenzoic acid (TIBA) induces floral bud initiation.—Auxins are known in general to inhibit



FIG. 23. Effect of SA alone and in combination with GA_3 on the growth and flowering of *Impatiens balsamina* L. under 24-hr photoperiods (LD). Plants receiving combination treatment are the longest, have more branches and bear the highest number of floral buds.

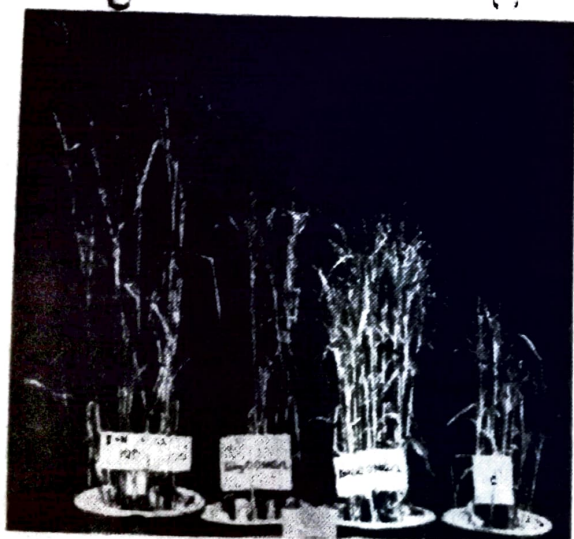


FIG. 24. Effect of β -N and GA_3 each alone and together on the growth and flowering of *Panicum miliaceum* under normal day (ND). Plants receiving combination treatment are the longest and bear more branches and ears.

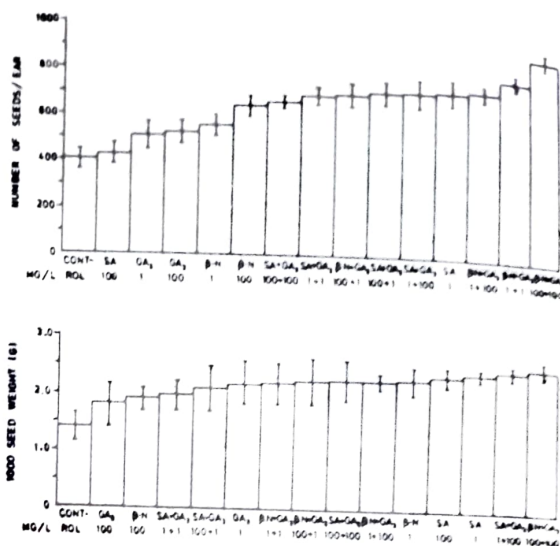


FIG. 25. Effect of GA_3 , SA and β -N, alone and in combination with each other, on the number of seeds/ear (top) and 1,000-seed weight (bottom) in *Setaria italica*. Vertical bars represent 95% level of confidence.

the flowering of short day plants. However, they do not affect the flowering of this plant; in fact they slightly delay floral bud initiation (Table X). TIBA which is considered to be an antiauxin is able to induce floral buds in this plant under strictly non-inductive photoperiods (Table XI). It would appear that this affect is caused by TIBA by lowering the level of endogenous auxins. But flowering in this plant is induced by GA_3 as well. This runs contrary to the assumption that floral bud initiation is controlled by the level of native auxin, as GA_3 is known to increase the level of endogenous auxins. Furthermore, it has been found that IAA inhibits GA_3 - as well as TIBA- induced flowering of this plant under non-inductive photoperiods (Sawhney et al. 1970, 1971). The fact that both GA_3 and TIBA are able to induce flowering in spite of their opposite effect on the level of endogenous auxins is suggestive that more than one pathway all ultimately leading to the transformation of the vegetative meristems into floral primordia may be involved.

Vitamins do not affect flowering.— Like auxins, vitamins also do not seem to affect floral bud initiation. Thus, α -tocopherol (vitamins E—animal fertility vitamin) does not affect, while ascorbic acid (vitamin C) delays floral bud initiation (Nanda et al. 1971; Nanda, 1972) in plants receiving 8 SD-cycles and completely inhibits in those receiving 4 SD

TABLE IX

EFFECT OF PURINE DERIVATIVES ON FLOWERING OF PLANTS RECEIVING INDUCTIVE AND NON-INDUCTIVE PHOTOPERIODS.

Treatment (10 mg/l)	Photo-period (h)	Days to floral bud initiation	Mean number of floral buds	Percent plants induced
Control		9.3	27.3	100
3' AMP	8	7.0	30.1	100
5' AMP		7.0	29.7	100
Cyclic AMP		7.6	26.4	100
Control		—	—	0
3' AMP	24	36.0	8.6	40
5' AMP		32.2	7.0	40
Cyclic AMP		34.0	8.0	40
Control		13.2	25.7	100
3' GMP	8	9.7	43.1	100
5' GMP		10.5	46.0	100
Cyclic GMP		9.7	38.0	100
Control		—	—	0
3' GMP	24	43.0	38.0	50
5' GMP		49.2	32.4	50
Cyclic GMP		43.0	41.6	80

Data from Nanda et al. (1976)

TABLE X

EFFECT OF EXOGENOUS APPLICATION OF AUXINS ON FLOWERING UNDER INDUCTIVE AND NON-INDUCTIVE PHOTOPERIODS.

Treatment (100 mg/l)	Photo-period (h)	Days to floral bud initiation	Mean number of floral buds	Percent plant induced
Control		14.5	15.2	100
IAA	8	17.0	12.5	100
IBA		16.0	16.6	100
2, 4—D		death	—	0
Control		—	—	0
IAA	24	—	—	0
IBA		—	—	0
2, 4—D		—	—	0

Data from Nanda et al. (1969)

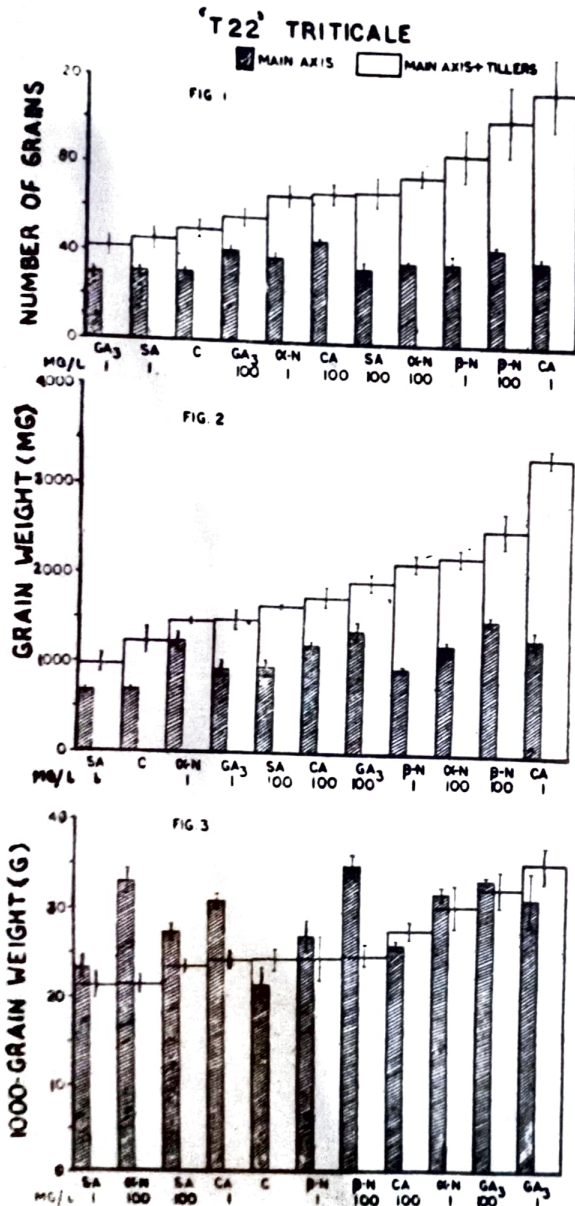


FIG. 26. Effect of α -naphthol (α -N), carboic acid (CA), β -naphthol (β -N), salicylic acid (SA) and gibberellic acid (GA_3) on the number of grains and the weight of all grains and 1,000 grains in the ears of the main axis (striped histograms) and per plant (broader empty histograms). Vertical bars represent 95% level of confidence.

cycles (Table XII). These results are not in accord with the 'ascorbic acid concept' of flowering put forth by Chinoy in 1969.

Phosphon D and cycocel affect the SD cycle requirement and also the critical photoperiod.—While abscisic acid, a naturally occurring growth inhibitory substance does not affect flowering, growth retardants phosphon D and cycocel which decrease extension growth, increase the dark period requirement. Thus, in plants treated with phosphon D, floral buds are not initiated under photoperiods beyond 14½ hr although 15½ hr is otherwise inductive. The number of SD cycles required to induce floral buds in cycocel-treated plants also increases to 5 instead of 3 in control. However, the number of floral buds and flowers increases in cycocel-treated plants exposed to 10 and 30 SD cycles (Nanda et al. 1967a, 1967b, 1968 and 1969). In marked contrast to this, morphactins, another group of synthetic growth substances which cause marked morphogenetic effects, decrease the number of floral buds and flowers under inductive photoperiods and it may be ascribed to the fact that leaf primordia during the development of buds fuse to cause malformations (Nanda et al. 1971).

Transmission of stimulus is controlled by source-sink relationship.—It is known that leaves are the organs of photoperception in plants and the flower inducing factor synthesized in the leaves is translocated in the plant to the meristems to cause differentiation. Experiments were carried out to study if the inductive effect of GA₃ treatment or of photoinduction given to one branch of two-branched balsam plants is transmitted to the other branch, which is maintained under non-inductive photoperiods. Surprisingly, the effect did not pass on to the untreated branch. The failure of the branch to flower even after

TABLE XI
EFFECT OF TIBA ON FLOWERING UNDER
INDUCTIVE AND NON-INDUCTIVE
PHOTOPERIODS.

Treatment (100 mg/l)	Photo-period (h)	Days to floral bud induction	Mean number of floral buds	Percent plants induced
Control	8	8.6±0.66	23.9	100
TIBA	8	8.2±0.54	17.7	100
Control	24	—	—	0
TIBA	24	55.0±0.54	5.0	50

Data from Sawhney et al. (1971)

TABLE XII
EFFECT OF ASCORBIC ACID (A) AND
α-TOCOPHEROL (B) ON FLOWERING OF
PLANTS EXPOSED TO DIFFERENT
PHOTOPERIODIC TREATMENTS.

Treat-ment	Photo-periods	Chemical	Days to floral bud induction	Mean number of floral buds
A	4 LD	Control	—	—
		Ascorbic acid	—	—
	4 SD	Control	14.0	3.8
		Ascorbic acid	—	—
	8 LD	Control	—	—
		Ascorbic acid	—	—
8 SD	Control	10.0	7.5	
	Ascorbic acid	13.0	4.3	
B	LD	Control	—	—
		α-tocopherol	—	—
	SD	Control	7.9	30.4
		α-tocopherol	7.2	34.3

defoliation can neither be ascribed to the production of inhibitor(s) by leaves on the branch under non-inductive photoperiods which, as is suggested by some workers, counteracts the effect of floral stimulus transmitted from the branch maintained under inductive photoperiods, nor to the interference in the transport of the stimulus from induced leaves to the bud. It is probably due to the fact that the flower inducing factor(s) synthesized in the leaves under inductive photoperiods is used up by axillary meristems and is, therefore, not available for transmission. Another experiment was therefore, performed in which the apices and axillary meristems on branches which were exposed to inductive photoperiods or were treated with GA_3 and maintained under non-inductive photoperiods, were excised. It was considered that if these axillary meristems act as sinks, their removal should prevent or reduce the local utilization of the stimulus. The removal of meristems on this branch and their retention on the other water-treated branch maintained under non inductive photoperiods, should strengthen the sink and accordingly should direct the stimulus to cause flowering of this branch. This is exactly what happens. This demonstrates that sink and source relationship are important in the transmission of the induction factor(s).

Another point that has emerged from these experiments is that in this plant while leaves are necessary for photoinduction, they are not necessary for GA_3 induction under non-inductive photoperiods (Sawhney et al. 1976). The non-specificity of plant organs to responded to GA_3 treatment is also apparent from the fact that GA_3 causes induction regardless of whether the treatment is given to the

growing apex or to any other part of the plant.

Metabolic drifts related to flowering.— Studies were then undertaken of metabolic drifts in the stem and leaves of plants maintained under inductive and non-inductive conditions. The results presented in figure 27 show that while the contents

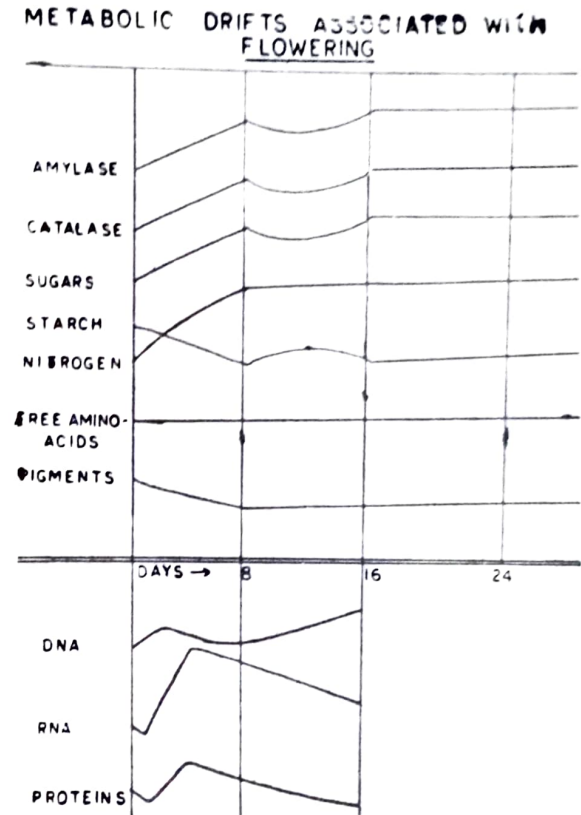


FIG. 27. Periodic changes in starch-, total sugar-, total nitrogen-, free amino acid-, DNA- and RNA contents of stem and leaves of *Impatiens balsamina* L. under 8 and 24 hr photoperiods.

of starch and polysaccharides decrease, that of sugars increases under inductive photoperiods (Sawhney et al. 1976). The activity of hydrolysing and oxidative enzymes also increases in plants under inductive photoperiods (Sawhney et al. 1970, Nanda et al. 1971). The content of soluble nitrogen decreases gradually while That of protein nitrogen and proteins decreases under inductive conditions (Kumar 1973) indicating enhanced incorporation of soluble nitrogen in the synthesis of proteins

concomitant with induction. DNA content is high initially and continues to increase in plants under inductive photoperiods probably due to an increase in the number of growth centres involving continued mitotic activity. RNA content also increases but the increase during 4-8 days is more under inductive than under non-inductive photoperiods. It would appear that with the induction of floral buds and consequent increase in the number of growth centres, the metabolic machinery is geared up to increase the mobilization of food material by increasing the activity of the degradative enzymes. Sugars so produced act as respiratory substrate for the increased release of energy that is needed for synthetic activity leading to the synthesis of proteins and nucleic acids to build up new cells and tissues.

The interesting point is that GA_3 which causes floral induction, also brings about similar metabolic changes in this plant even under non-inductive photoperiods (Sawhney et al. 1976).

Protein metabolism and isoenzyme patterns also change with induction. There is a marked increase in the protein content of leaves which are photoperceptive organs (Kumar 1973). The difference in the qualitative pattern of proteins of the leaves of plants under inductive and non-inductive photoperiods and the appearance of a new protein band with high electrophoretic mobility in the stem of plants (Fig. 28) is also significant and are suggestive that apart from the increase in the turn-over of protein synthesis, the qualitative changes in proteins may also be involved in the inductive process (Kumar 1973).

This is also apparent from investigations on changes in the activity of enzymes and isoenzyme patterns of amylase, catalase and peroxidase under inductive and non-

inductive photoperiods. The inductive photoperiods cause the synthesis of new isoamylase (Rf 0.05) in both the stem and the leaves (Fig. 29). This isoenzyme is synthesized even under non-inductive photoperiods in plants treated with either GA_3 or GA_{13} which also induce floral buds indicating its association with floral induction. The appearance of an additional

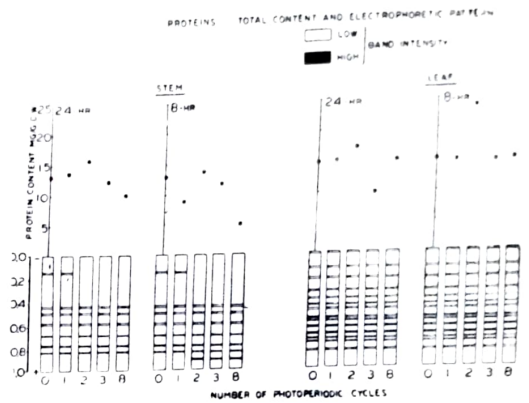


FIG. 28. Total content and polyacrylamide gel electrophoretic pattern of water soluble proteins in the stem and the leaves of *Impatiens balsamina* under 24 and 8 hr photoperiods. D. W. stands for dry weight and N for a new protein band.

isoenzyme in the leaves of plants regardless of gibberellin and photoperiodic treatments is indicative that it may not be involved in flowering. Induction of this isoenzyme in the stem and not in the leaves by GA_3 suggests that it may be concerned with the mobilization of reserve food materials to make them available for growth (Tiwari 1975).

Changes in RNA pattern associated with induction.—Changes in isoenzyme patterns described in the previous section can be possible only if new RNAs are released. A preliminary experiment demonstrated new bands of RNA in both the stem and leaves of plants exposed to inductive photoperiods (Fig. 30) suggesting that qualitative alterations in the information molecules are involved in induction process (Sharma et al. 1976).

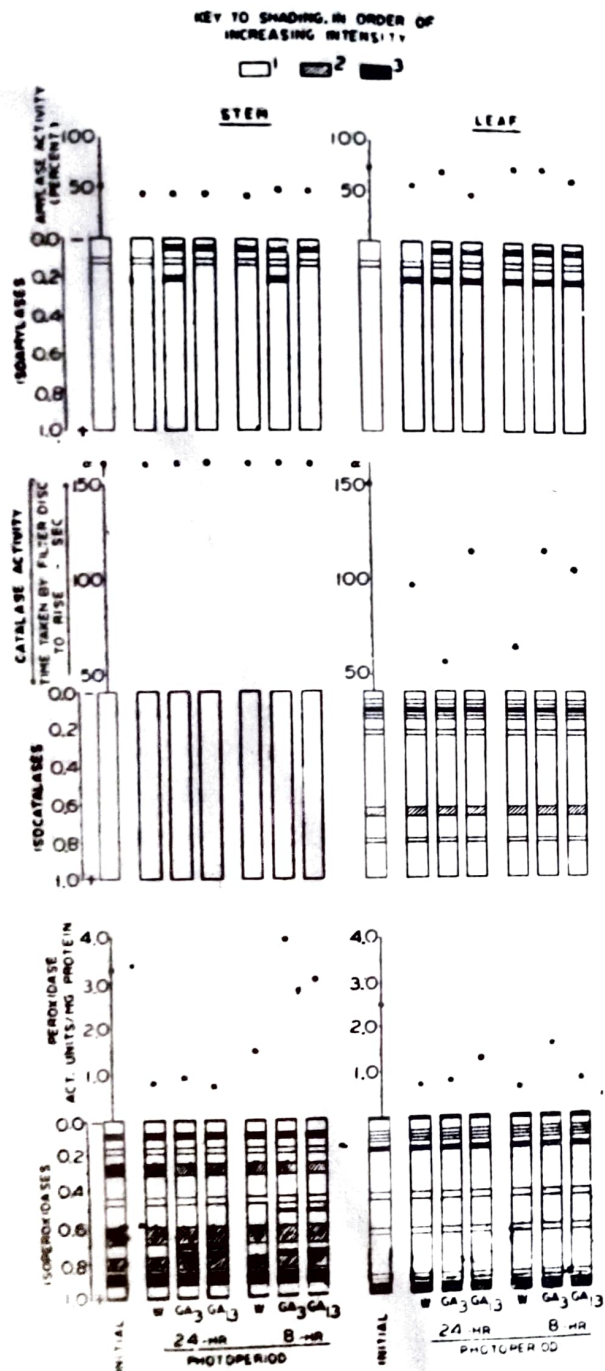


FIG. 29. Total amylase, catalase and peroxidase activities and the electrophoretic patterns of isoamylases, isocatalases and isoperoxidases after 20 days in the stem and the leaves of water and 10 mg/l GA₃ and GA₁₃-treated plants exposed to 24- and 8-hr photoperiods.

Metabolic inhibitors affect flowering differently.—An alternative approach to understand the mode and extent of involvement of protein and nucleic acid metabolisms in flowering is the use of metabolic inhibitors. Experiments carried out to study their effect reveal that the

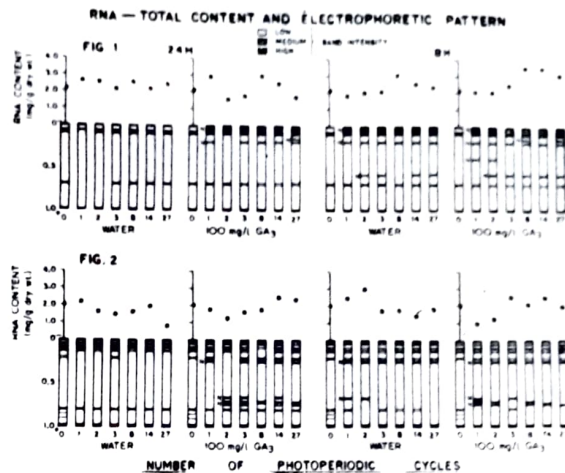


FIG. 30. Total content and electrophoretic pattern of RNAs in the stem and the leaves of *Impatiens balsamina* treated with water and 100 mg/l GA₃ and exposed to 24- and 8-hr photoperiods. N₁ and N₂ stand for new RNA bands.

effect of inhibitors is different on photo- and GA₃—caused induction (Table XIII). Thus, chloramphenicol and actinomycin-D hasten floral bud initiation and increase the number of floral buds under inductive photoperiods but do not affect the GA₃-caused induction under noninductive photoperiods. On the other hand, while cycloheximide hastens (Nanda et al. 1973), FU and FUDR completely inhibit the GA₃—caused induction under non-inductive

TABLE XIII

EFFECT OF METABOLIC INHIBITORS ON PHOTO- AND GA₃-CAUSED INDUCTION

Metabolic inhibitors	Photo-induction	GA ₃ -induction
<i>Protein inhibitors</i>		
Chloramphenicol	promotion	no effect
Cycloheximide	no effect	promotion
<i>RNA inhibitors</i>		
5-FU	no effect	inhibition
Act-D	promotion	no effect
<i>DNA inhibitors</i>		
5-FUDR	no effect	inhibition

Data from Kumar (1973).

conditions but do not affect it under inductive photoperiods. These observations are suggestive of some difference in the nature of induction caused by the two factors.

The more interesting part is that cycloheximide increases the number of leaves and enhances even the increase caused by GA_3 (Fig. 31). This behaviour of cycloheximide in hastening GA_3 -caused flowering and promoting morphogenesis in general, is rather paradoxical. This stimulatory effect can be brought about either by inhibition

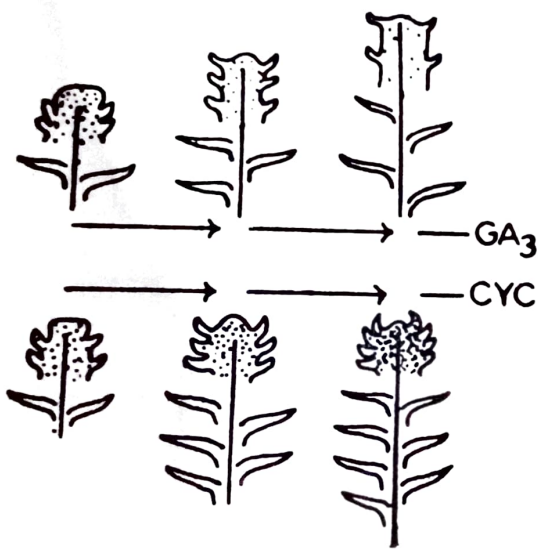


FIG. 31. Diagrammatic representation of the apical meristem showing the temporary nature of stimulated leaf differentiation caused by GA_3 due to enhanced rate of elongation but the permanent increase in the number of leaves caused by cycloheximide.

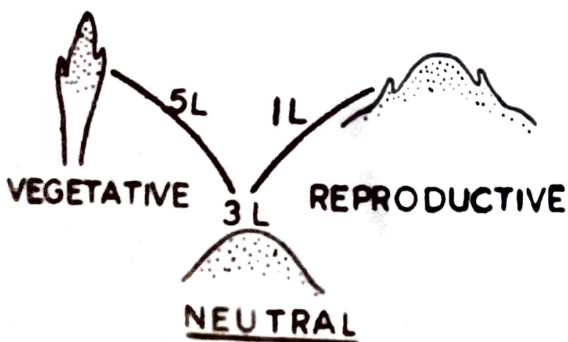


FIG. 32. Diagrammatic representation of 'neutral meristem' at 3 lux and its differentiation into vegetative under 5 lux but into reproductive bud under 1 lux of light.

of some inhibitory factor(s) which may be proteinaceous in nature or by affecting some cellular metabolism other than protein synthesis e. g., respiratory activity (Nanda et al. 1973).

The preceding discussion on the physiology of flowering and its relation to growth pattern in balsam and other plants, although has not brought out a flow sheet of events morphological, physiological or molecular which transform vegetative meristem into flowers, has brought out a number of unique aspects which, if manipulated properly, can lead to a better understanding of this complex morphogenetic phenomenon. Our achievement in inducing balsam plants with neutral meristems (Nanda et al. 1970) may prove particularly useful for this purpose. This condition is attained when plants are exposed to a light intensity of 3 lux. The axillary meristems under this light condition remain undifferentiated. At lower light intensities the axillary meristems become reproductive while at higher intensities they develop into vegetative branches (Fig. 32).



FIG. 33. Effects of β -N and GA_3 alone and in combination with each other on the vegetative growth and flowering of *Panicum miliaceum* under 24-hr photoperiod (LD). The grain yield of plants treated with the combination was the highest. The control (c) plants did not flower under this photoperiod.

Our achievement in inducing balsam and other plants to flower under all conditions is not only of fundamental importance but is of great practical

significance and is useful in horticulture, forestry, plant breeding and most of all to the common man as it may help in increased crop productivity (Fig. 33).

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