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The Effect of Photoperiod on Lateral Shoot Development in *Dianthus caryophyllus* L. cv. Improved White Sim[1]

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Abstract. **Long photoperiods (either naturally long days or 4-hour night interruptions with low intensity incandescent light) inhibited lateral shoot development and induced early flowering in perpetual flowering carnation *(Dianthus caryophyllus)*. Short photoperiods delayed flowering but enhanced lateral shoot development only when shoots were vegetative. Once a shoot was induced, short photoperiods had no influence on time to terminal shoot flower or on subtending vegetative lateral shoot development. Vegetative lateral shoot development was inhibited by night interruption lighting regardless of light source. These data indicate that high flower production in spring and summer is due to lateral vegetative shoots which begin elongation and growth during the non-flower inductive short days of winter. At higher latitudes low production of flowers may not entirely be due to low photo-synthetic light but to the low number of lateral shoots. This low number of potential flowering shoots is due to highly inductive long days of summer which have caused shoots to flower before subtending lateral shoots can begin growth for future flower production.**

The perpetual-flowering carnation is classified as a faculatative short night plant as flower initiation is delayed by short photoperiods (1, 5). Irradiating plants with low intensity incandescent light during the night has been shown to induce both early flower initiation and a more uniform flowering date among shoots as compared to plants not irradiated (normal day photoperiods) or grown under short photoperiods (1, 3, 5, 9, 10, 17).

At least 4 to 7 expanded leaf pairs must be present on the shoots for rapid flower induction when shoots are irradiated with low intensity night lighting (6, 16). Although shoots which have been lighted flower earlier than non-lighted shoots, they have less lateral branching (9, 10, 15). The latter is undesirable, as an active growing lateral branch, 5 cm long, will flower 30 to 60 days earlier than a lateral branch which was not elongating at the time the flowering shoot was removed (13). Carnation plants grown under short photoperiods develop many lateral branches compared to plants grown under long photoperiods, but flowering under short photoperiods is greatly delayed (17). Heins and Wilkins (8) indicated that short photoperiods prior to floral initiation stimulated lateral branching and delayed flowering, but, when given after floral initiation had occurred, short days had no effect on lateral branching.

Light quality influences lateral branching, as red (R) light has been shown to promote lateral branching while far red (FR) light inhibits lateral bud release and subsequent growth (12, 18). Although a mixture of R and FR light promotes flower induction more than either light quality by itself (7, 19), no studies on the effect of light quality have been conducted on lateral branching in carnation. In the present study, we conducted 2 experiments to determine the effects of photoperiod and light quality on flowering and lateral branching in the carnation.

Materials and Methods

Experiment I: Rooted 'Improved White Sim' carnation cuttings were benched in a 1 soil:1 peat:1 perlite (by volume) medium on September 1, 1975. All were grown under normal photoperiods (N) at 45°N latitude until the terminal growing points were removed on September 21. Fifteen similar plants were placed under each of the following treatments: 1) normal (N) daylength (fall/winter/summer: 12 hr 0 min to 8 hr 46 min to 15 hr 37 min), 2) short (S) photoperiod (8 hr: shade cloth pulled 1600 to 0800), or 3) night interruption lighting from 2200 to 0200 with either cool white fluorescent (FL) (2.5 μW cm^{-2} 650 to 700 nm, 0.8 μW cm^{-2} 700 to 750 nm) incandescent light (INC) (24.5 μW cm^{-2} 650 to 700 nm, 31.6 μW cm^{-2} 700 to 750 nm), or FR light from a BCJ ruby red bulb (4.1 μW cm^{-2} 650 to 700 nm, 10.1 μW cm^{-2} 700 to 750). Light measurements were made with an ISCO Spectroradiometer Model SR (Instrumentation Specialties Co., Lincoln, NE). The plants were grown under the respective photoperiod treatments until the experiment was terminated on June 21, 1976.

Temperatures were maintained at 16.5°C day, 12.5°C night or as close to these temperatures as possible with fan and pad cooling. Nutrients were applied when required as determined by soil analysis. Lateral shoots developing from the original cutting were called primary (1°) shoots, while those shoots that developed on the primary shoots were called secondary (2°) shoots. Data included the number of days to flower and the number of 2° vegetative shoots longer than 2 cm present on the 1° shoot at flowering. Flower stems were harvested by cutting the internode below the 7th leaf pair from the flower. The 2° shoots were allowed to flower and similar data were recorded.

Experiment II: Rooted cuttings were planted in 7.5 cm plastic pots on May 10 and repotted to 12.7 cm pots on June 24, 1976. Medium, temperature and fertility were as in Expt. I. The plants were grown under normal daylength until the terminal growing point was removed 14 days later leaving the plants with 4 nodes; uniform plants with 4 primary vegetative lateral shoots were selected. Sufficient plants were grown so that 5 plants per treatment were available for sampling at each of 11 sampling periods.

Photoperiod treatments were 1) normal (N) daylength (spring/summer/winter: 14 hr 39 min at potting to 15 hr 37 min to 8 hr 46 min), 2) short (S) days (as in Expt. I), or 3) long (L) days (INC light as in Expt. I). Treatments were as outlined in Fig. 1, showing the photoperiodic sequences to which the plants were subjected. At the respective sampling times (Fig. 1) 5

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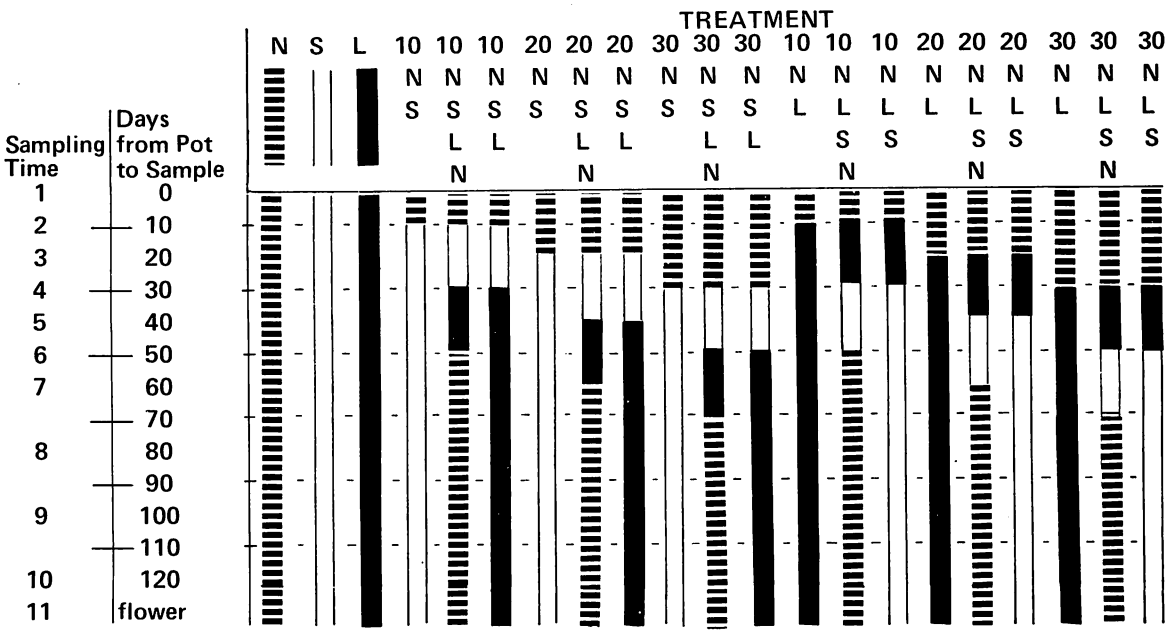

Fig. 1. Photoperiod treatments given to carnation plants during Expt. II. Photoperiods were normal daylength (N), short photoperiods (S) (black cloth 1600 – 0800), and long photoperiods (L) (night interruption with incandescent light from 2200 – 0200). Plants that were grown for either 10, 20 or 30 days under N are designated as 10 N, 20 N or 30 N. The next letter or letters indicates subsequent photoperiod treatment lengths. Intermediate letters indicate 20 day treatment periods. The terminal letters indicate the subsequent photoperiod treatment used until flowering.

plants from each treatment were removed and the following data recorded: number of visible leaf pairs and total number of nodes, the length of the 1° shoots from their base to their meristem apex and longest leaf, the length of the 2° buds at all nodal positions, and 1° and 2° shoots were classified as vegetative or reproductive. Days to flower were calculated. The number of 2° vegetative shoots greater than 2 cm long on the last date of sampling (Period 11, Fig. 1) was recorded. The 1° apical shoot was defined as shoot 1 and the 1° basal shoot as shoot 4. Five plants were allowed to flower for all treatments. At flowering, the apical node of each flowering shoot was designated as nodal position 1 with subtending nodes being consecutively numbered. This allowed comparisons of 2° bud growth at uniform nodal positions below the flower.

Table 1. Influence of photoperiod treatments on time to flower and on the number of vegetative shoots greater than 2 cm long present at flowering. Expt. I started September 1, 1975.

	No. flowers cut/plant		No. vegetative 2° shoots		Days to flower	
Treatment[z]	Flush 1[y]	Flush 2	Flush 1	Flush 2	Flush 1	Flush 2
ND	4.0[x]	5.7	4.2 c[w]	0.5 a	194 c	252 a
SD	4.0	–	6.3 d	–	216 d	–
FL	4.5	3.4	2.3 b	0.6 a	179 b	249 a
INC	4.5	3.4	1.4 a	0.8 a	162 a	249 a
FR	4.3	3.8	2.9 b	0.9 a	172 b	250 a

[z]N = Normal day; S = Short day; FL, INC, FR = Night interruption from 2200 to 0200 with cool white fluorescent light (FL) (2.5 μW cm^{-2} 650 – 700 nm, 0.8 μW cm^{-2} 700 – 750), incandescent (INC) (24.5 μW cm^{-2} 650 – 700 nm, 31.6 μW cm^{-2} 700 – 750 nm), or BCJ Ruby Red incandescent lamp (FR) (4.1 μW cm^{-2} 650 – 700 nm, 10.1 μW cm^{-2} 700 – 750), respectively.

[y]Flush 1 was the first group of shoots to flower after the original pinch (1° shoots). Flush 2 was the second group of flowers which developed from the lateral shoots (2° shoots) which were present when the first flush of flowering shoots were removed or developed later.

[x]No estimate of error was available to make comparisons among the no. flowers cut/plant means.

[w]Mean separation, within columns by Tukey's HSD test, 5% level.

Results

Experiment I.

The 1° shoots from treatments which flowered earliest had fewer 2° shoots than those that flowered later (Table 1). The 1° shoots in the INC treatment flowered earliest and had the fewest 2° shoots. The differences in days to flower and number of 2° laterals on 1° shoots irradiated with the FL and FR light sources were not significant. Primary shoots under S photoperiods formed the greatest number of 2° shoots but flowering was significantly delayed. The 1° shoots on plants grown under N daylengths developed during the winter when the daylength was 8 hr 45 min or longer. Days to flower and 2° lateral shoot formation were intermediate to those under the S or L photoperiods.

The 2° lateral shoots remaining on the plants after the first flush of flowers were cut developed during the spring when the light spans were lengthening, and flowered during the long light spans of May and June (15 hr 37 min on June 21). No significant differences occurred in either days to flower or number of laterals formed on the 2° shoots between the N daylengths and any of the night interruption treatments. Source of light had no differential effect on 2° branching or days to flower. Flowering of 2° lateral shoots was delayed under the S photoperiod treatment, and flowering did not occur by 270 days when the experiment was terminated.

Experiment II.

General trends. Long days induced early flowering and inhibited 2° shoot elongation whereas S photoperiods delayed flowering and stimulated 2° shoot formation (Table 2). Plants grown under N daylengths were intermediate in their response Regardless of photoperiod, the shoots remained vegetative until at least 12 to 14 nodes were present. Then flower induction was dependent upon the photoperiod under which the

Table 2. Influence of normal, short and long photoperiods during the growth of carnation plants on the number of days for shoots to flower, number of nodes present on primary shoots at the time of flowering and number of vegetative secondary shoots 2 cm or longer at time of flowering. Expt. II started May 10, 1977.

Treatment code[y]	No. of days to flower				No. of nodes on primary shoots at time of flower				No. of vegetative secondary shoots ⩾ 2 cm at time of flower			
	Nodal position[z]				Nodal position[z]				Nodal position[z]			
	(apical) 1	2	3	(basal) 4	(apical) 1	2	3	(basal) 4	(apical) 1	2	3	(basal) 4
Flowered under normal photoperiods												
N	121	135	146	227	17.8	18.4	20.2	23.8	5.0	3.2	3.0	4.0
10 NLSN	104	126	174	276	14.0	16.6	20.4	25.5	0.4	1.6	1.8	4.4
20 NLSN	109	113	109	172	14.4	15.2	16.3	18.8	2.2	1.0	2.6	2.2
30 NLSN	114	117	122	–[x]	15.2	16.0	17.6	–[x]	2.4	1.2	2.4	–[x]
10 NSLN	121	129	173	234	16.2	18.0	20.2	22.6	1.2	2.0	2.4	4.2
20 NSLN	–	–	–	–[x]	–	–	–	–[x]	–	–	–	–[x]
20 NSLN	–	–	–	–	–	–	–	–	–	–	–	–
Flowered under short photoperiods												
S	248	281	285	292	25.0	27.4	26.6	27.8	5.8	6.6	7.2	8.0
10 NS	241	273	274	286	23.8	28.0	27.5	28.0	7.0	8.0	6.4	6.4
20 NS	260	267	285	293	27.0	28.4	28.8	28.2	9.4	8.6	4.2	7.2
30 NS	255	276	251	291	28.0	28.0	27.2	28.0	7.8	8.6	9.6	5.8
10 NLS	104	105	267	265	14.0	15.0	27.5	28.3	1.4	0.6	5.8	4.8
20 NLS	110	110	269	275	14.6	14.6	27.0	28.0	1.6	1.0	5.6	6.4
30 NLS	116	126	120	269	15.8	16.8	16.3	28.5	1.2	1.0	1.0	7.0
Flowered under long photoperiods												
L	89	95	119	134	13.4	14.8	16.6	18.4	0.4	0.8	0.6	0.2
10 NL	97	101	108	154	14.2	14.4	15.8	19.0	0.2	0.0	0.0	0.8
20 NL	106	102	119	142	15.0	15.4	16.6	17.0	0.6	0.8	0.0	0.0
30 NL	114	120	109	199	15.4	17.0	17.0	21.8	0.8	0.4	0.2	1.4
10 NSL	121	119	132	141	16.2	17.4	17.8	18.5	0.2	0.4	0.2	0.4
20 NSL	128	136	140	198	17.2	17.8	19.0	20.8	0.6	0.6	0.2	0.6
30 NSL	134	137	148	160	18.0	18.6	19.0	19.0	2.4	0.8	0.8	0.6
Significant differences[w]	35 (5%), 46 (1%)				3.2 (5%), 3.7 (1%)				2.1 (5%), 2.8 (1%)			

[z]Shoot 1 is the apical primary shoot on the plant, shoot 4 is the basal.

[y]Treatment code: The designations N, S, or L indicate continuous normal day, short day (black cloth 1600 – 0800), or long day (night interruptions of incandescent light from 2200 – 0200); 10 N, 20 N or 30 N indicate 10, 20 or 30 days of normal photoperiods; the last letter in any sequence indicates that photoperiod under which the shoots flowered; any intermediate letter or letters indicate a period of 20 days of L and/or S.

[x]No data available because of sampling error.

[w]Differences between any 2 means must be greater than the indicated values to be significantly different based on single degree of freedom F tests.

plant was grown and the nodal position of the shoot on the plant.

Primary shoots developing from the apical nodal position initiated flowering stems with fewer nodes present than 1° shoots from the basal nodal position (Table 2, treatments N, S, and L). The time to flower was correspondingly increased for shoots from the basal nodal position. Except under S treatments, the number of vegetative 2° shoots present on shoots at flowering decreased from the apical to the basal nodal position.

Plants transferred from N to S photoperiods. Plants transferred to the S photoperiod after 10, 20 or 30 days of N daylength responded similarly to plants continuously grown under a S photoperiod treatment. They exhibited delayed flowering with many vegetative 2° shoots (Table 2).

Plants transferred from N to L photoperiods. Plants transferred to the L photoperiod after 10, 20, or 30 days of N photoperiod responded similarly to plants that were continuously grown under the L photoperiod treatment. They flowered early, had very low node number, and had low vegetative 2° shoot number. Increasing the number of days under N photoperiods before transfer to the L photoperiod, however, resulted in trends where flowering was delayed, node number and the number of vegetative 2° shoots increased although the differences between means in many cases were not significant.

Plants transferred from N to S to L photoperiods. Plants grown under a S photoperiod for 20 days in addition to the 10, 20 or 30 days of N daylength (Treatments 10 NSL, 20 NSL and 30 NSL) exhibited trends similar to the NL treatments. Transferring the plants to L photoperiods 10 and 20 days later than the treatment 10 NSL resulted in differences between means which were non-significant. However, we feel these trends which existed where flowering was delayed (Table 2) node number and the number of 2° shoots increased are meaningful.

Secondary shoot growth was inhibited to some extent on all shoots that developed and flowered under continuous L photoperiod. The upper two 1° shoots of plants in 10 NSLN which were transferred to N after 20 days each of S and L

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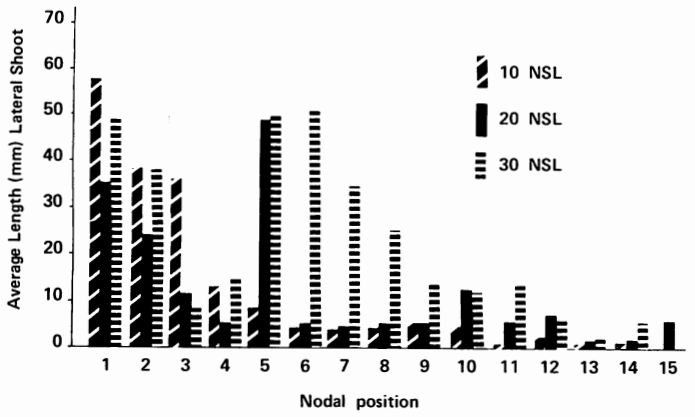

Fig. 2. Development of secondary lateral shoots on the apical primary shoot of plants with 4 primary shoots. Plants were grown under normal photoperiods for 10, 20 or 30 days (10 N, 20 N or 30 N), then for 20 days under short photoperiods (S) and subsequently under long days (L) until the primary shoots flowered. The secondary bud immediately subtending the flower was designated as nodal position 1. Expt. II.

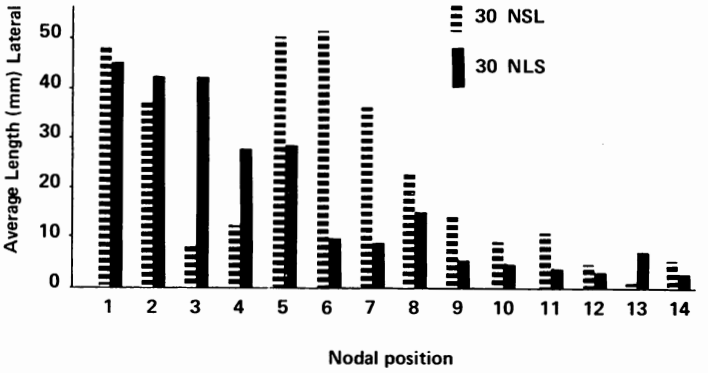

Fig. 4. Development of secondary lateral shoots on the apical primary shoot of plants with 4 primary shoots. Plants were grown under normal photoperiods for 30 days (30 N), then short days (S) or long days (L) for 20 days, and subsequently under L or S until flowering occurred. The secondary bud immediately subtending the flower was designated as nodal position 1. Expt. II.

photoperiods flowered at approximately the same time as the two upper 1^{o} shoots of treatment 10 NSL, and had approximately the same number of nodes (Table 2). However, the two upper 1^{o} shoots of treatments 10 NSLN had 1.0 and 1.6 more 2^{o} shoots at time of flowering than the 1^{o} shoots of 10 NSL. Because of a sampling error, no data are available for treatments 20 NSLN and 30 NSLN. Primary shoot 2 from the 20 NSL treatment flowered at the same time and had about the same number of nodes as shoot 2 of treatment N plants. However, the N plants had 2.6 more 2^{o} shoots than the 30 NSL plants, showing continued L photoperiods or I irradiation inhibited 2^{o} shoot elongation.

Plants transferred from N to L to S photoperiods. The 1^{o} shoots from apical nodal positions initiated flowers at an earlier developmental stage than 1^{o} shoots from a basal nodal position. Thus, 1^{o} shoots from the basal nodal positions of plants which were transferred from L to S photoperiods took longer to flower, and had significant increases in the number of nodes and number of active 2^{o} shoots. For example, under treatments 10 NLS, 20 NLS and 30 NLS (Table 2), flower buds were initiated on the upper 1^{o} shoots under the L photoperiod and the 1^{o} shoots flowered in 100 to 125 days. Flower initiation did not occur on the lower 1^{o} shoots under the L photoperiod, and thus, when these shoots were transferred to the S photoperiod, they did not flower until approximately 150 days later. Along with this delay, a concomitant increase in number of nodes present on these shoots at flowering occurred. The basal 1^{o} shoots also produced significantly more vegetative 2^{o} shoots 2 cm or longer than the apical 1^{o} shoots. The transfer from L to S photoperiod did not delay the flowering data on the upper 1^{o} shoots which had initiated flower buds under the L photoperiod (Table 2: compare shoots 1 and 2 of 10, 20 and 30 NL with 10, 20 and 30 NLS).

Comparison of vegetative 2^{o} shoot length. The data in Table 2 show the number of 2^{o} shoots greater than 2 cm long on 1^{o} shoots at time of flowering, but do not show differences in length of 2^{o} shoots at similar nodal positions when the 1^{o} shoots flowered. The effect of delaying the advent of L photoperiods can be seen by comparing treatments 10 NSL, 20 NSL and 30 NSL. The 4 nodes subtending the flower formed reproductive 2^{o} shoots while the remaining 2^{o} shoots were vegetative. Very little vegetative 2^{o} shoot growth occurred on 1^{o} shoots under treatment 10 NSL while considerable growth occurred at node 5 on 1^{o} shoots under treatment 20 NSL (Fig. 2). Delaying the start of L photoperiods for 10 additional days (treatment 20 NSL vs. 30 NSL) resulted in 2^{o} shoot growth increases at nodes 5 to 8.

Short day treatments had little, if any, effect on 2^{o} shoot elongation if the S photoperiods were given early in development of a 1^{o} shoot (10 NSL) or if they were given after a 1^{o} shoot had initiated a flower (10 NLS) (Fig. 3). Delaying L photoperiod and floral induction resulted in significant increases in 2^{o} shoot growth (30 NSL) (Fig. 4). Again, S photoperiods following L photoperiods had little effect on 2^{o} shoot growth (30 NLS) once floral induction had occurred.

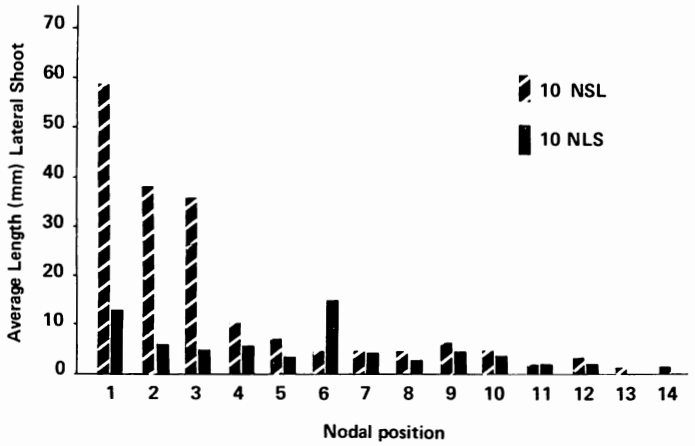

Fig. 3. Development of secondary lateral shoots on the apical primary shoot of plants with 4 primary shoots. Plants were grown under normal photoperiods for 10 days (10 N), then short days (S) or long days (L) for 20 days, and subsequently under L or S until flowering occurred. The secondary bud immediately subtending the flower was designated as nodal position 1. Expt. II.

Discussion

Many of the previous photoperiod studies on carnation flowering have neglected to report the effects of photoperiod on vegetative 2^{o} shoot development (1, 3, 5, 6). Other studies have shown that 2^{o} shoot development is inhibited by low intensity incandescent lighting during the night (10, 14, 15).

A 4-hr night interruption has been reported to almost entirely inhibit 2^{o} shoot elongation (15). Continuous dusk to dawn lighting significantly reduced 2^{o} shoot formation compared to cyclic lighting (1 min cycles) during the same period (14). Porkorny and Kamp (17) reported that plants grown under S photoperiods formed flowering stems with many vegetative 2^{o} shoots while stems from plants grown under a 16 hr photoperiod had very few active 2^{o} buds or shoots. Our previous (8) and current results using a night interruption of INC concur with these observations that 2^{o} shoot development is inhibited by night lighting with INC light and is stimulated by S photoperiods (Table 1, 2).

Based on these studies and our observations of 2^{o} shoot growth, we present the following model of 2^{o} shoot development and flowering in the carnation. A developing carnation shoot remains vegetative until at least 12 to 14 nodes are present. After this stage of development, floral initiation is dependent upon photoperiod. Under S photoperiods, floral induction is delayed while under L photoperiod, it is hastened. During the initial vegetative growth stage, very little 2^{o} shoot elongation from any lateral bud is observed until after the 12 to 14 nodes are present, suggesting strong apical dominance. Phillips (16) reported on similar inhibitions of 2^{o} shoot development until at least 10 nodes had formed.

After this stage, lateral bud growth can be observed at many of the nodes subsequently formed if the shoot remains vegetative. Once the 2^{o} shoots start elongating, they frequently continue elongating even after floral initiation of the 1^{o} shoot has occurred and these 2^{o} shoots are present and elongating at flowering of the 1^{o} shoot. It appears that after 12 to 14 nodes have formed on the 1^{o} shoot, apical dominance is reduced and 2^{o} shoot growth can then begin. Perhaps these 2^{o} shoots develop into a sink for metabolites which they can maintain even after floral initiation on the 1^{o} shoot. It follows that, after initiation, the flower bud may re-establish apical dominance and becomes a dominant sink over non-actively growing subtending lateral buds. These lateral buds would be inhibited from further growth. This would explain why S photoperiods stimulates 2^{o} shoot development before floral induction but not afterward.

This model suggests that photoperiod is the dominant factor in controlling branching. This is supported by the results in Expt. I (Table 1) where the second flush flowering shoots under FL (high R:FR) had no more 2^{o} shoots present than the high FR:R irradiated plants (INC or BCJ). In addition, an earlier paper by Heins and Wilkins (8) showed that photoperiod was the predominant influence on branching.

It is interesting to correlate flower production with photoperiod. Production tends to follow the total solar radiation curve, decreasing in winter and increasing in spring and summer (2). However, since it takes 5 to 6.5 months for a 2^{o} shoot to flower under N conditions (11), it is obvious to us that the 2^{o} shoots of the low winter production period started to elongate during the long photoperiods of summer and the larger spring and summer production started elongation under the S photoperiods of winter. This supports the model that L photoperiods, which hasten flower initiation, inhibits 2^{o} shoot growth while S photoperiods, which delay flower initiation, stimulates 2^{o} shoot growth.

A comparison of treatments 10 NSLN and 10 NSL (Table 2) suggest that irradiation with incandescent light (high FR:R) over an extended time period inhibits further 2^{o} shoot development. Any irradiation with incandescent light may significantly decrease 2^{o} shoot formation. Thus, 1^{o} shoot 1 on plants growing under N daylength flowered at the same time as shoot 1 on treatment 10 NSL and 10 NSLN plants, but had significantly more 2^{o} shoots at time of flowering. This inhibition of 2^{o} shoot development by incandescent light (high FR) concurs with reports on other plants (12, 18).

Frequently, commercial greenhouses receive carnation plants from the propagator which are reproductive or become reproductive shortly after planting. This early flower initiation decreases the number of potential nodes from which vegetative shoots and subsequent future flower production arises after the apical growing point is removed. Vegetative plants from the propagator would insure adequate vegetative nodes so that a large number of 1^{o} shoots are present. Cuttings are removed from the stock plants continually during the winter and spring months and stored in coolers until needed for rooting in May and June. By May and June, the natural days are long and many of the cuttings probably initiate flowers while rooting under N photoperiods. The use of S photoperiods while rooting should ensure vegetative cuttings so that higher flower yields would be possible.

Short photoperiods may also be of value in maintaining stock plants in a vegetative condition while the last cuttings are being removed in April and May. This could be especially important in high latitudes such as Northern Europe where photoperiods become long in the spring. Cuttings shipped from the United States to Columbia during the summer have been reported to us to produce superior plants compared to those from the Netherlands while the opposite is true in the winter (personal communication: Dan Gelfman, Miami, Florida). While other factors certainly may be involved during both seasons (4), the best cuttings come from the country (latitude) that had the shorter photoperiod at the time.

Single cropping of carnations may be economically feasible under certain conditions such as growing a crop of carnations for a particular holiday. The use of S photoperiods could insure vegetative plants with many 1^{o} shoots. These plants could then be lighted giving long days to induce rapid uniform flowering for a particular date. Further, these data indicate that a 4 hr night interruption irradiance with incandescent light is effective in inducing carnation flower initiation. Dusk to dawn lighting, while very effective at inducing floral initiation may inhibit 2^{o} lateral shoot growth even more than night interruption, and requires considerably more electrical energy.

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