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Induction of fertile flowers in potato (*Solanum tuberosum* L.) by silver thiosulphate anionic complex

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Summary

The effect of gibberellic acid containing mixtures, silver thiosulphate and extended photoperiod on flowering induction in 16 non-flowering potato genotypes and on flowering enhancement in 14 normally potato flowering genotypes was studied in sub-tropical plains of India during short-day autumn crop season of 2000–2001 and 2001–2002. Extended photoperiod alone was not successful in induction of flowering. Silver thiosulphate in combination with extended photoperiod effectively induced flowering in 16 potato genotypes studied for flowering induction. Induced flowers of some genotypes were male fertile. Normal berry setting was observed on induced flowers and seeds obtained from such berries germinated normally. Gibberellic acid containing treatments were not very effective in flower induction as they induced some flowering only in few genotypes. In the normally flowering genotypes silver thiosulphate enhanced maximum flowering and duration of flowering to a great extent.

Abbreviations: STS, silver thiosulphate; FD, flowering duration; MF, maximum flowering

Introduction

Potato flowers under long days, moderate temperature and high humidity. Though flower primordia of potato can rise in total darkness (Jones & Borthwick, 1938), a photoperiod of 14–18 hours and night temperatures of 15–20 °C favours flower production and berry setting in potato (Almekinders, 1992). In tropics and sub-tropics, conditions conducive to flowering and fruiting are available only at high altitude (>1500 m above mean sea level) when the crop is grown during summer season. Short-day environment suppresses flowering of potato. Most Indian cultivars, many being European subsp. *tuberosum* in origin, would not flower under short day conditions in Indian plains, where the potato is a winter crop, but flower in the hills, where it is a summer crop, grown under longer days (Pushkarnath, 1976). Temperature conditions also influence photoperiodic response. Although, most of the genotypes flower in the hills of northern India, but wide variability has been observed for this character and some genotypes do not flower even under best of conditions. Contrarily, some genotypes even flower under short day conditions in the plains (Birhman & Kaul, 1989). Profuse flowering in the hills has made it possible to execute potato breeding projects, which may otherwise have been difficult if the choice was restricted only to the plains. In the sub-tropical plains of India, flowering could be induced in some genotypes using extended photoperiod and gibberellic acid (GA_3) containing mixtures, with auxin (2,4 D) (Gopal & Rana, 1988); and with auxin (IBA) and cytokinin (kinetin) (Khan et al., 1994). GA_3 in combination with Gapol (a mixture of various elements with auxin indole acetic acid) was found beneficial in flower development in a non-flowering cultivar Marijke in Mexico

(Lozoya-Saldaña & Miranda-Velázquez, 1987). Hoekstra (1989) also found beneficial effect of GA_3 alone in enhancing flowering in a normally flowering accession. There is need to find out some other treatments which can produce flowering in recalcitrant genotypes to make it possible to carry out hybridization work for breeding projects in plains without much limitation. In the present study various GA_3 containing hormonal treatments and a non-hormonal treatment with silver thiosulphate were tried with and without extended photoperiod for induction and enhancement of flowering in potato.

Materials and methods

The plant material consisted of 16 non-flowering genotypes (Set I genotypes) and 14 flowering genotypes (Set II genotypes). Set I genotypes normally develop some buds but do not flower under short days subtropical plains of India, while set II genotypes produce flowers under such conditions. The set I and set II genotypes were grown on 1 October of 2000–2001 and 2001–2002 autumn crop seasons at the Central Potato Research Station Jalandhar (31°02′N, 75°02′E, 237 m above mean sea level). The data on minimum and maximum temperature and humidity on daily basis are given in Table 1. The non-flowering genotypes studied for flowering induction were: JEB/A 53, EB/C 899, JE 812, QB/A 9–120, Craigs Defiance, JEX/A 751, PH/F 1545, CP 3142, CP 1338, CP 3165, MS/92–1090, CP 3088, E 4451, JTH/C 107, Kufri Badshah and JEX/B 998. The flowering genotypes studied for flowering enhancement were: CP 1458, JX 1, JN 1197, CP 2283, JEX/A 528, J.92–159, CP 1659, JX 161, JX 90, JEX/A 1192, JI 1857, JW 160, JX 115 and Kufri Ashoka. Genotypes JEX/A 751, JEX/B 998, JEX/A 528 and JEX/A 1192 were Andigena accessions (*Solanum tuberosum* subsp. andigena) while all other genotypes studied were Tuberosum *(Solanum tuberosum* subsp. tuberosum) accessions. Separate experiments were carried out with set I and set II genotypes. Planting of genotypes was done in randomised complete block design with split plot with three replications. Photoperiod was main-plot treatment with genotypes and chemical treatments as sub-plot treatments. Main plots consisted of normal photoperiod and extended photoperiod. The extended photoperiod of 17 hours per day was created by artificial illumination in continuation to the natural photoperiod at sunset with 250 W high pressure sodium vapour lamps erected at a height of 3.6 m above the ground, one bulb being sufficient for 100 m^2. Under both extended and normal photoperiod, for each genotype seven rows per replication, each row consisting of 4 plants, were planted at plant to plant and inter-row spacing of 20 cm and 60 cm, respectively. The six rows of a genotype were given 6 different chemical treatments while seventh row (control) was not given any chemical treatment. The chemical treatments were applied by spraying on foliage thoroughly in morning hours at weekly interval from bud initiation stage. Polythene sheets were used as barriers between rows while spraying chemicals to prevent drifting of chemical treatments to neighboring rows. The various chemical treatments used in the present study were:

T1 = GA_3 (gibberellic acid)(50 ppm) + BAP (6-benzylaminopurine) (4 ppm) + IBA (indole-3-butyric acid) (10 ppm);
T2 = GA_3 (50 ppm) + BAP (4 ppm);
T3 = GA_3 (50 ppm) + kinetin (6-furfurylaminopurine) (4 ppm) + IBA (10 ppm);
T4 = GA_3 (50 ppm)+ kinetin (2 ppm)+IBA (10 ppm);
T5 = GA_3 (50 ppm) + 2,4 D (2,4 dichlorophenoxyacetic acid) (50 ppm) + kinetin (4 ppm);
T6 = STS (silver thiosulphate) (2 mM Ag^+)

Some earlier studies reported induction of flowering in few potato genotypes using GA_3 in combination with auxin (2,4 D or IBA) and/or cytokinin (kinetin). These treatments along with some modifications of these treatments and STS were tried in order to find out a treatment which can induce or enhance flowering in large number of genotypes. STS solutions were prepared immediately before use by adding excess sodium thiosulphate to silver nitrate solutions, so that the equilibrium reaction was shifted towards the $Ag(S_2O_3)_2^{3-}$ complex. Observations were recorded on days to bud initiation, days to flower initiation, flowering duration and maximum flowering per plant. Days to buds

Table 1. The temperature and humidity during autumn crop season of 2000–2001 and 2001–2002

	Range for daily temperature		Range for daily humidity (%)	
Crop season	Maximum	Minimum	Maximum	Minimum
2000–2001	18–33 °C	3.5–17 °C	75–87	48–70.8
2001–2002	14.5–29.0 °C	6–17 °C	67–85	43–66.0

Table 2. Flowering induction in normally non-flowering (set I) genotypes by silver thiosulphate treatment

Genotype	Flowering duration (days)			Maximum flowering (flowers per plant)		
	Extended photoperiod	Normal photoperiod	Mean	Extended photoperiod	Normal photoperiod	Mean
JEB/A 53	37.3	34.2	35.7	15.7	12.3	14.0
EB/C 899	21.8	18.3	20.1	19.8	10.2	15.0
JE 812	15.7	5.2	10.5	10.7	3.6	7.1
QB/A 9-120	36.8	14.5	25.7	24.8	7.0	15.9
Craigs Defiance	17.2	0.0	8.6	11.5	0.0	5.7
JEX/A 751	28.0	0.0	14.0	8.7	0.0	4.3
PH/F 1545	17.7	10.0	13.8	15.2	4.8	10.0
CP 3142	26.5	0.0	13.2	28.0	0.0	14.0
CP 1338	7.4	0.0	3.7	8.2	0.0	4.1
CP 3165	19.3	0.0	9.6	17.5	0.0	8.7
MS/92-1090	22.8	0.0	11.4	20.3	0.0	10.1
CP 3088	11.0	0.0	5.5	10.2	0.0	5.1
E 4451	31.2	23.2	27.2	19.5	13.3	16.4
JTH/C 107	31.2	25.0	28.1	23.7	9.7	16.7
Kufri Badshah	19.8	0.0	9.9	13.5	0.0	6.7
JEX/B 998	19.5	0.0	9.7	17.8	0.0	8.9

initiation were considered from planting date to the time floral bud reached a diameter of about 1 mm. Pollen fertility was observed by staining the fresh pollen with 2% acetocarmine. The induced flowers were pollinated with highly fertile pollen of normally flowering genotypes to test the berry setting and seed production. The true seeds extracted from the berries so obtained were treated with 2000 ppm GA_3 and sown in boxes containing 1:1 mixture of sand and farmyard manure to test their viability.

Statistical analysis

The data were pooled over years and analysis of variance for set II genotypes was done according to randomized complete block design with split plot (Gomez & Gomez, 1984).

Results

Extension of photoperiod alone was not successful in induction of flowering in non-flowering potato genotypes. STS was the most effective chemical treatment in induction of flowering in non-flowering genotypes. Flowering could be induced in all normally non-flowering genotypes namely JEB/A 53, EB/C 899, JE 812, QB/A 9–120, Craigs Defiance, JEX/A 751, PH/F 1545, CP 3142, CP 1338, CP 3165, MS/92–1090, CP 3088, E 4451, JTH/C 107, Kufri Badshah and JEX/B 998 with STS treatment in combination with extended photoperiod (Table 2). STS treatment was able to induce flowering in genotypes JEB/A 53, EB/C 899, JE 812, QB/A 9–120, PH/F 1545, E 4451 and JTH/C 107 without the extension of photoperiod. However MF in these genotypes was comparatively better under extended photoperiod. The range over genotypes for MF per plant induced by STS under extended and normal photoperiods were 8.2–28.0 and 0.0–13.3 flowers per plant, respectively. The durations of flowering induced by STS for genotypes under extended and normal photoperiod ranged from 7.4–37.3 and 0.0–34.2 days, respectively. Treatment T3 (GA_3, 50 ppm + kinetin, 4 ppm+IBA, 10 ppm) induced flowering in the genotype JEB/A 53 both under normal (MF = 1.7 flowers per plant, FD = 6.8 days) and extended photoperiod (MF = 7.3 flowers per plant, FD = 16.7 days). T3 also induced flowering in CP 3165 under extended photoperiod (MF = 4.1 flowers per plant, FD = 9.2 days). Another chemical treatment T1 (GA_3, 50 ppm + BAP, 4 ppm + IBA, 10 ppm) induced flowering in genotype EB/C 899 both under normal (MF = 7.5 flowers per

plant, FD = 11.3 days) and extended photoperiod (MF = 7.5 flowers per plant, FD = 15.3 days). Other chemical treatments were not effective in inducing flowering in any genotype. STS treatment was able not only to induce good flowering, but also helped in retaining the flower fertility and berry setting. The STS induced flowers of JE 812, Craigs Defiance, PH/F 1545, CP 3142, CP 3165, MS/92–1090, CP 3088, JTH/C 107 and Kufri Badshah were found to be male fertile by acetocarmine staining. However, flowers of genotypes JEB/A 53, EB/C 899, QB/A 9–120, JEX/A 751, CP 1338, E 4451 and JEX/B 998 were not pollen fertile. The seeds extracted from the berries obtained by pollination of STS induced flowers germinated normally.

Error variances were homogeneous over years for set II genotypes for all the 4 characters. Hence, results are presented based on pooled analysis of data over two years (crop seasons). Analysis of variance in split-plot design for various characters of normally flowering (set II) genotypes with photoperiod as main-plot treatment and genotypes and treatments as sub-plot treatments are presented in Table 3. Year had significant effect on days to bud initiation. Bud initiation was not affected by photoperiod. Photoperiod had significant effect on days to flowering initiation, FD and MF. Genotypes and chemical treatments had significant effect on all the four characters namely days to bud initiation, days to flower initiation, FD and MF. Photoperiod × genotype, photoperiod × chemical treatment, genotype × chemical treatment and photoperiod × genotype × chemical treatment interactions were significant for all the 4 characters except genotype × chemical treatment interaction for MF.

In set II genotypes, flowering initiation was earlier by about 5 days under extended photoperiod (Figure 1). Overall increase in MF and FD due to extension of photoperiod was 50.4% and 53.2% respectively. MF and FD were significantly high over control in all chemical treatments (Figure 2). However there was very high increase in MF and FD due to STS treatment. Genotypes also differed significantly for both MF and FD (Table 4). The mean MF and FD for genotypes over all treatments ranged from 5.4 to 34.6 flowers per plant and from10.4 to 64.1 days, respectively. STS increased mean FD and MF by 76.5% and 140.5%, respectively. All the set II genotypes had enhanced FD and MF by the treatment of STS. Per cent increase in FD and MF by STS was very high in genotypes having poor flowering compared to profusely flowering genotypes.

Table 3. Analysis of variance of normally flowering (set II) genotypes for 4 characters

		Mean square for character[a]			
Source	*df*	BI	FI	FD	MF
Year	1	3222**	2.50	7.67	1.28
Replications in years	4	1.09	0.88	1.13	3.54
Photoperiod	1	0.02	1728**	1687**	1170**
Year × photoperiod	1	54.6**	0.50	10.1	1.10
Error	4	1.24	1.75	1.80	1.57
Genotypes	15	3206**	898**	231**	50.7**
Year × genotypes	15	324**	20.4**	9.18**	6.15**
Photoperiod × genotypes	15	14.7**	85.0**	26.3**	15.4**
Year × photoperiod × genotypes	15	9.68**	16.3**	9.64**	5.73**
Treatments	6	47.6**	11890**	6019**	2585**
Year × treatment	6	2.81**	1.30	6.34*	0.54
Photoperiod × treatment	6	2.37**	1491**	1359**	1054**
Year × photoperiod × treatment	6	2.56**	6.82**	7.33*	1.38
Genotypes × treatments	90	4.99**	540**	165**	39.4
Year × genotypes × treatments	90	3.46**	17.7**	13.1**	6.49**
Photoperiod × genotypes × treatments	90	3.99**	72.1**	34.1**	17.8**
Year × photoperiod × genotypes × treatments	90	3.07**	16.9**	8.75**	5.49**
Error	888	0.69	0.90	2.65	0.81

*,**significant at $p \leq 0.05, 0.01$, respectively.

[a]BI, days to buds initiation; FI, days to flowering initiation; FD, flowering duration (days); MF, maximum flowering (flowers per plant).

Discussion

The present study demonstrated that extension of photoperiod alone was not enough for induction of flowering in non-flowering potato genotypes and that the plants require additional chemical treatments. This is in agreement with earlier studies (Gopal & Rana, 1988; Khan et al., 1994) on flower induction in potatoes growing on the Indian plains. STS in combination with extended photoperiod was successful in induction of

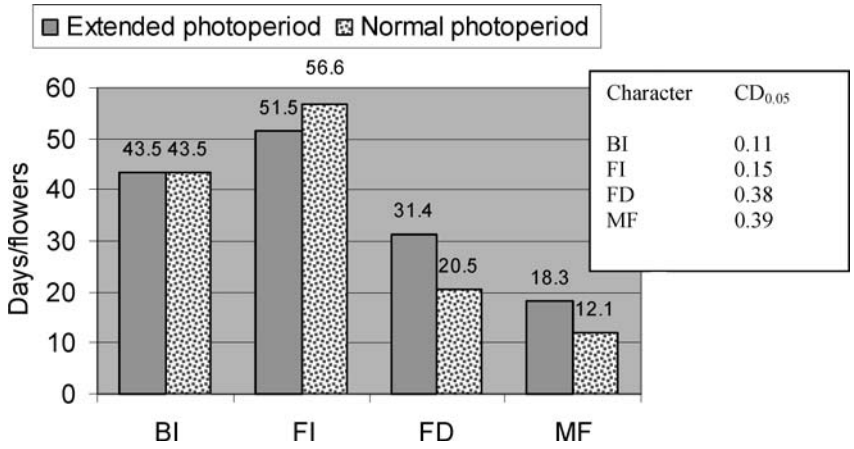

Figure 1. Effect of photoperiod on days to bud initiation (BI), days to flowering initiation (FI), flowering duration in days (FD) and maximum flowering (flowers per plant) (MF) in normally flowering (set II) genotypes.

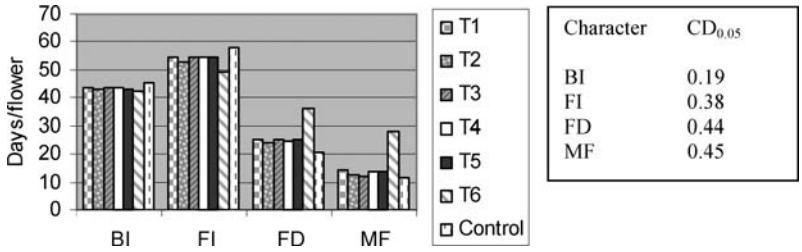

Figure 2. Effect of chemical treatments on days to bud initiation (BI), days to flowering initiation (FI), flowering duration in days (FD) and maximum flowering (flowers per plant) (MF) in normally flowering (set II) genotypes.

flowering in all 16 non-flowering genotypes. This is in marked contrasts with the results of Hoekstra (1989), who reported no effect of STS in promoting flowering in a sparsely flowering Andigena accession under long days in Federal Republic of Germany. In the present study flowering could be induced even in the Andigena accessions namely JEX/A 751 and JEX/B 998. The differences in results may be due to environmental conditions or due to the specific genotypes studied. GA_3 containing hormonal treatments induced flowering only in three genotypes. In Indian plains, Gopal and Rana (1988) induced flowering in five genotypes with repeated spray of GA_3 (50 ppm) and 2,4 D (50 ppm) in combination with extended photoperiod. Khan et al. (1994) were able to induce flowering in cultivar Kufri Bahar under subtropical Indian plains with extended photoperiod in combination with spray of GA_3 (50 ppm), IBA (10 ppm) and kinetin (2 ppm). Various methods such as planting on bricks, removal of tubers and spray of gibberellic acid have been suggested for induction of flowering in non-flowering genotypes (Pushkarnath, 1976), although the success of these treatments is not guaranteed (Sadik, 1983).

The STS induced flowers of some genotypes were male fertile, while flowers of genotypes JEB/A 53, EB/C 899, QB/A 9–120, JEX/A 751, CP 1338, E 4451 and JEX/B 998 were pollen sterile. The male sterility of these genotypes was genetically controlled as these genotypes are also known to produce sterile pollen even under long-day conditions in hills of northern India, where these genotypes flower naturally (personal observation). Flowers induced by earlier workers (Lozoya-Saldaña & Miranda-Velázquez, 1987; Gopal & Rana, 1988; Khan et al., 1994) using GA_3 containing treatments were either sterile and/or did not set berries. The flower sterility observed by these workers may be due to hormonal imbalance.

In present study, photoperiod had significant effect in enhancing flowering in normally flowering genotypes by decreasing days to flowering initiation, and increasing FD and MF. However, extension of photoperiod alone was not successful in induction of flowering in non-flowering genotypes. The work of west-European and north-American breeders particularly that in heated glasshouse during winter in 1940's and 1950's, showed the importance of photoperiod

Table 4. Effect of various chemical treatments* and genotypes on flowering duration and maximum flowering of normally flowering (Set II) genotypes

	Flowering duration (days)								Maximum flowering (flowers per plant)							
Genotype	T1	T2	T3	T4	T5	T6	C	Mean	T1	T2	T3	T4	T5	T6	C	Mean
CP 1458	16.9	27.1	18.3	29.2	27.4	43.6	27.2	27.2	8.7	10.5	10.7	18.1	5.7	28.0	13.0	13.5
JX 1	27.7	28.6	26.2	28.8	38.9	44.2	28.6	31.9	40.5	35.7	18.1	28.9	36.2	53.9	29.2	34.6
JN 1197	33.6	32.2	36.3	32.7	36.3	42.7	33.3	35.3	20.8	16.6	18.7	28.3	30.7	40.5	26.1	26.0
CP 2283	21.1	11.2	11.2	11.1	11.4	24.1	11.2	14.5	16.4	2.2	2.5	2.4	2.3	22.1	2.4	7.2
JEX/A 528	14.8	10.1	20.5	17.9	20.1	30.3	12.0	18.0	6.7	5.2	7.6	5.2	7.0	14.6	5.8	7.5
J.92-159	37.7	25.2	45.4	28.9	20.3	44.0	20.8	31.8	18.7	19.0	19.6	19.1	16.9	31.9	9.3	19.2
CP 1659	12.1	17.2	15.8	17.1	16.8	25.5	8.7	16.2	5.2	10.4	14.2	9.1	9.7	24.2	4.8	11.1
JX 161	53.2	57.7	53.0	55.5	58.1	58.7	46.4	54.7	32.2	20.0	12.2	21.2	23.1	42.9	21.7	24.8
JX 90	65.9	66.0	66.5	64.4	62.9	65.2	57.5	64.1	28.5	28.5	34.3	36.3	28.7	49.5	27.8	33.4
JEX/A 1192	13.5	10.0	10.5	10.3	10.4	23.5	10.7	12.7	8.2	4.2	4.6	4.2	4.1	23.4	7.3	8.0
JI 1857	22.2	17.2	17.1	19.2	14.8	29.9	11.3	18.8	3.9	3.4	4.2	4.2	4.7	15.0	2.3	5.4
JW 160	20.0	15.4	11.5	11.6	11.5	28.2	6.4	15.0	5.5	5.1	5.2	5.7	6.1	10.7	3.6	6.0
JX 115	12.0	12.6	15.5	10.2	10.1	24.7	7.2	13.2	1.7	6.8	10.5	8.0	7.4	19.6	3.6	8.2
Kufri Ashoka	2.7	9.6	9.1	12.1	14.0	20.0	5.1	10.4	1.7	9.6	9.2	2.2	8.7	14.0	5.8	7.3
Mean	25.2	24.3	25.5	24.9	25.2	36.0	20.4		14.2	12.7	12.2	13.8	13.7	27.9	11.6	
$CD_{0.05}$ for genotypes								0.62							0.63	
$CD_{0.05}$ for treatments				0.44								0.44				
$CD_{0.05}$ for genotype × treatment				1.64								1.66				

*T1, GA_3 (50 ppm) + 6-benzylaminopurine (4 ppm) + 3-indole butyric acid (10 ppm); T2, GA_3 (50 ppm) + 6-benzylaminopurine (4 ppm); T3, GA_3 (50 ppm) + kinetin (4 ppm) + 3-indole butyric acid (10 ppm), T4, GA_3 (50 ppm) + kinetin (2 ppm) + 3-indole butyric acid (10 ppm); T5, GA_3 (50 ppm) + 2,4 D (50 ppm) + kinetin (4 ppm); T6, Silver thiosulphate (2 mM Ag^+).

for flowering in potato, but did not produce conclusive information on photoperiodic response of flowering (see Burton, 1989). Martins and Pinto (1994) in Brazil found extension of photoperiod upto 40 days from emergence useful in induction of flowering in potato cultivar Monalisa. Lozoya-Saldaña and Miranda-Velázquez (1987) reported beneficial effect of extended photoperiod in favouring bud retention. Photoperiod controls several responses like flowering and tuber formation. Martínez-García et al. (2002) showed that *Arabidopsis thaliana* CONSTANS (AtCO), a flowering-time gene which accelerate flowering in response to long days, impairs tuberization in potato (*Solanum tuberosum* subsp. andigena) under short day inductive conditions. AtCO over expressing lines required prolonged exposure to short days to form tubers. Genotypes in present study differed significantly for flowering characters such as FD and MF. Flowering had been shown to be genetically controlled (Mishra & Kishore, 1966).

There was very high increase in MF and FD in normally flowering genotypes due to STS treatment. STS increased mean MF by 140.5% over the untreated control. The enhancement of flowering by more than 50% in a well flowering potato accession was also reported by Hoekstra (1989). The changes in FD and MF by GA_3 containing hormonal treatments (other than STS treatment) were, however, comparatively less and inconsistent over genotypes. Flowering enhancement by GA_3 was also reported in cultivar Marijke (Lozoya-Saldaña & Miranda-Velázquez, 1987). The enhancement of flowering by STS in well flowering potato accessions was also reported by Hoekstra (1989). Hoekstra (1989) found that in normally flowering potato accessions STS improve seed production by raising the fruit setting and number of seeds per berry. The increase in MF by STS was due to both increased number of inflorescences and number of flowers per inflorescence. The increase in number of flowers per plant principally because of more inflorescence positions has been reported earlier (Almekinders, 1992; Almekinders & Struik, 1996).

In the present study STS was found useful for both flowering induction in non-flowering genotypes

and flowering enhancement in normally non-flowering genotypes. Silver ions as silver nitrate has been used to induce perfect flowering in many cucurbits like Cucumber (Peng et al., 2000) and muskmelon (Owens et al., 1980). $AgNO_3$ and STS were used to induce male flowers in gynoecious cucumbers (Nijs and Visser, 1980; Scurtu and Scurtu, 1995) and genetically female *Cannabis sativa* (Ram and Sett, 1982). Scurtu and Scurtu (1995) found that while induction of male flowers in cucumber with gibberellins had negative effects as it elongate internodes and causes plant yellowing while silver nitrate could be used for the purpose without such negative effects. The silver ion was found to be a potent inhibitor of ethylene action (Beyer, 1976). Veen and van de Geijn (1978) demonstrated that STS inhibit ethylene production in cut carnations, thereby increasing their longevity. The silver ions present here as apart of an anionic complex, mostly $Ag(S_2O_3)_2^{3-}$, which increases its mobility in plant and might also reduce its phytotoxicity. Ram and Sett (1982) also found that application of silver in the anionic complex is more effective than in cationic form in induction of flowering.

Flowering of large number of genotypes, flower fertility, berry setting and viable seed production are required for the execution of hybridization programme under short-day conditions, such as the plains of India. The results of the present study show that STS can induce flowers in large number of non-responsive genotypes without affecting pollen fertility and with good berry setting and viable botanical seed production.

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