Leaf Abscission Induced by The Iodide Ion [1]

Richard A. Herrett, Herbert H. Hatfield, Jr.,
Donald G. Crosby [2], & A. J. Vlitos [3]
Union Carbide Chemicals Co., Agricultural Research Station, Clayton, N.C.

Introduction

In the course of biological screening for herbicidal activity in synthetic compounds, various organic iodide complexes had marked defoliating properties when applied to leguminous test plants. Simple iodides such as the salts of alkali metals also caused defoliation. Although this effect has been reported in the patent literature (4, 8), our present investigation was undertaken principally to learn more about some of the factors influencing iodide induced abscission as well as the relationship between this effect and the general problem of foliar abscission.

Materials & Methods

Laboratory reagent grade chemicals were generally employed as the source of the iodide ion. In some instances, however, various organic iodide complexes were synthesized and purified in the laboratory. Concentrations ranging from 0.44 to 7.35 $\times$ 10^{-2} M of the iodide ion in tap water containing 0.05 % by weight of Triton X-155 caused effective defoliation when applied to plant foliage. However, rates at the lower end of this range (0.44 to 2.94 $\times$ 10^{-2} M) induced effective leaf drop and were used in most of the experiments.

The defoliant solutions were sprayed onto test plant foliage using a Beltsville type conveyer belt sprayer equipped with a No. 6502 or No. 6503 standard Tee-jet nozzle. The speed of the conveyer belt was adjusted so that leaves were wet to incipient run-off.

Unless otherwise indicated, the test plants were *Phaseolus vulgaris* var. Tendergreen. Six to eight bean seeds were planted per 4 inch pot in a composted light loam type soil. Uniformity was achieved by thinning to between three and five plants per pot prior to treatment. Treatments were usually applied when the primary leaves were 50 to 60 mm long and prior to the expansion of the first trifolate. This stage was between 10 and 11 days after planting. The percentage defoliation was obtained by counting the number of primary leaves which abscised for each plant and calculating the percentage abscission on the basis of the total number of primary leaves in that pot. The data are averages of between three and five replicate pots which comprised each treatment.

The plants were grown under 16 hours of light either artificially supplied by a combination of fluorescent and incandescent lamps providing approximately 1,000 ft-c at plant level or in the greenhouse with supplementary incandescent lamps to provide the difference between natural day length and a day length of 16 hours.

Results

Indicated in table I are data supporting the point made in the introduction; organic iodide complexes are capable of inducing premature abscission of Tendergreen bean leaves. The data also support the point that simple inorganic iodide salts of alkali metals such as sodium and potassium also cause premature abscission. From field experiments, this phenomenon was demonstrated on field-grown beans.

In order to establish whether or not iodide ion was the only halide capable of causing defoliation, solutions of KI, KBr, KCl, and NaF were sprayed

Table I

Abscission of Leaves of Mature Tendergreen Bean Plants by Various Organic Iodide Complexes & Inorganic Iodide Salts

Compound name	Iodide conc $\times$ 10^{-2} M	% Defoliation
Methylisothiouronium iodide	5.65	80
Dibutyl butylamidophosphate magnesium diiodide	4.47	73
	2.24	17
Dibutyl butylamidophosphate zinc diiodide	4.17	83
	2.09	80
Dibutyl butylamidophosphate cobaltous diiodide	4.24	90
	2.12	93
Potassium iodide	7.35	97
	3.68	93
Sodium iodide	8.20	97
	4.10	97
Untreated control	...	10

[1] Received revised manuscript Dec. 8, 1961.

[2] Present address: University of California, Davis, Cal.

[3] Central Agricultural Research Station, Caroni Limited, Carapichaima, Trinidad, West Indies.

Table II

Effect of Various Halogens on Abscission of Primary Leaves of Tendergreen Beans

Halogen salt	Halogen conc ($\times$ $^{-2}$ M)	% Defoliation
KI	0.74	90
	1.47	0*
	2.94	0*
	7.35	0*
KBr	1.03	0
	2.05	0
	4.10	0
	10.25	0
KCl	1.65	0
	3.30	0
	6.60	0
	16.50	0
NaF	2.92	0
	5.83	0
	11.66	0
	29.15	0**

* Leaves severely desiccated and frozen on the stem.
** Slight marginal burning.

on bean plants. Only the iodide ion induced defoliation (table II). Desiccation and freezing which prevent defoliation were a result of excessive concentrations of the iodide ion and will be discussed below in more detail. The only other response to these halides was slight marginal burning at the highest concentration of NaF.

The application of the iodide ion was followed by an apparent desiccation of the leaf blades. This generally was visible 24 to 48 hours following application and increased in severity until the leaf abscised. The petiole also became yellowish with a sharp line appearing at the base of the pulvinus. The proximal side of this line appeared relatively normal.

The various oxidation states of iodine were examined (table III). All solutions were made up to contain iodine in amounts equivalent to that contained in KI when applied at the concentrations indicated. All were aqueous solutions with the exception of elemental iodine which was dissolved in a solvent system containing 2.5 % methanol, 2.5 % diethylether, 2.5 % glycerine, and 92.5 % water. The ability of I_2 to induce abscission supports the contention of a recent patent (8). The oxidation state of iodine

Table III

Influence of Iodine Oxidation State on Abscission of Tendergreen Bean Leaves

Iodine compound	% Defoliation							
	6 Days after treatment Iodide conc ($\times$ 10^{-2} M)				14 Days after treatment Iodide conc ($\times$ 10^{-2} M)			
	0.19	0.37	0.74	1.47	0.19	0.37	0.74	1.47
KI	0	100	61*	25*	6	100	72*	30*
I_2	0	61	88*	61*	61	100	100	100
KIO_3	61	44	39*	67*	78	61	39*	94*
H_5IO_6	6	11	28*	44*	22	61	61*	61*

* Remaining leaves severely desiccated and frozen on the stem (see text).

Table IV

Effect of Various Salts on Abscission of Primary Leaves of Tendergreen Beans

Iodide salt	% Defoliation							
	4 Days after treatment Iodide conc ($\times$ 10^{-2} M)				8 Days after treatment Iodide conc ($\times$ 10^{-2} M)			
	0.74	1.47	2.94	7.35	0.74	1.47	2.94	7.35
CdI_2	83	89	100	89	89	89	100	89*
ZnI_2	78	94	83	0	78	94	83	0*
NaI_2	72	83	88	11	100	100	72	17*
MgI_2	33	67	78	6	94	100	83	6*
KI	50	78	61	0	94	100	78	0*
NH_4I	22	50	39	0	94	89	50	0*
AlI_3	0	0	0	0	33	72	100	94*
CaI_2	17	28	39	0	50	72	39	17*
FeI_2	0	0	0	0	100	100	100	0*
$(CH_4)_4NI$	0	0	0	0	17	61	94	61*

* Leaves severely desiccated and frozen on the stem.

appears to influence the induction of premature abscission. The lower oxidation states are the most effective.

When various iodide salts were applied, it was found that the cation influenced the rate and degree of defoliation. Again, all solutions were made up to contain equivalent amounts of iodine based on the amount contained in the KI solutions. Table IV indicates the influence of the cation on the time and extent of response. Defoliation by aluminum, ferrous, and tetramethylammonium iodides was much slower than that caused by the potassium salt, although all of the compounds showed some abscission 8 days following treatment. The calcium cation caused a marked reduction in the percentage of defoliation both 4 and 8 days following application.

To determine if penetration through the roots followed by translocation through the stem would induce defoliation similar to that obtained with foliar treatment, solutions (50 ml) containing KI (200, 20, & 2 mg) were applied to the soil. Complete defoliation of primary leaves was observed at the 2 mg level. At the 20 and 200 mg/pot rate, desiccation and freezing due to excessive concentrations were observed. The results of foliar and soil applications are shown in figure 1.

When KI was applied to just one of the two primary leaves, it was observed that only the treated leaf abscised, whereas the opposite, untreated, leaf remained intact and showed no indications of injury. This result, with that of the soil application, indicate that the iodide ion is effectively transported upward, but that probably little or no translocation occurs downward out of the treated leaf or through the phloem.

Excessive concentrations of iodide ion caused leaf desiccation and freezing on the plant without defoliation (note, for example, the lack of abscission at higher concentrations in foliar and soil treatment, (fig 1). This effect was explored further by placing plants which had been excised at the soil level in beakers containing various concentrations of the iodide ion for either 3 or 24 hours. They were then removed, thoroughly washed, and placed in distilled water. Figure 2 shows the defoliation 8 days after treatment. Both durations of immersion indicate an optimum concentration of KI above which freezing of the leaves was observed. In the case of 3-hour immersion, the concentration was above 1,000 ppm; in the case of 24-hour immersion, it was above 125 ppm.

In those instances where excessive concentrations of the iodide ion resulted in desiccation followed by freezing, it was noted that the terminal meristem was killed. The possibility that an interaction existed between an active meristem and the point of abscission was examined. The terminal meristem was removed before, during, and after the application of KI (Iodide conc 2.94×10^{-2} M). Table V shows the reduction in defoliation when decapitation occurred at the time of treatment or within 4 days. Later decapitation was without effect.

In the preceding experiment, the single decapitation was followed by subsequent growth of axillary buds. These secondary buds apparently had replaced

Table V

Effect of Decapitation on Abscission of Primary Leaves of Tendergreen Bean Plants Treated With KI*

Time of decapitation	% Defoliation Days after treatment		
	2	4	6
48 hr prior to treatment	11	100	100
24 hr prior to treatment	11	78	100
Day of treatment	6	50	100
24 hr after treatment	33	78	100
48 hr after treatment	50	100	100
Non-decapitated	56	100	100

* Iodide concentration 2.94×10^{-2} M

Table VI

Effects of Removing Terminal & Secondary Buds on Abscission of Primary Leaves of Tendergreen Beans Induced by KI*

Treatment	% Defoliation Days after treatment		
	2	4	7
Decapitated & KI	0	11	11
Non-decapitated & KI	56	100	100
Decapitated control	0	0	0
Non-decapitated control	0	0	0

* Iodide concentration 2.94×10^{-2} M

Fig. 1. Effect of foliar and soil applications on KI on defoliation. *Left to right*: Untreated controls. Foliar application of 0.74, 1.74, 2.94, and 7.35×10^{-2} M. Iodide as KI application of 2, 20, and 200 mg of KI in 50 ml. of water.

Fig. 2. Effect of various iodide concentrations on excised bean plants immersed in solutions for 3 and 24 hours. *Extreme left*: Untreated control. *Upper row*: From left to right—62.5, 125, 250, 500, 1,000, and 2,000 ppm of KI for 3 hours. *Bottom row*: From left to right—concentrations as in the upper row immersed for 24 hours. Photo taken 8 days after beginning of the treatments.

Fig. 3. Effect of 2,3,5-triiodobenzoic acid (TIBA) on Tendergreen beans. *Left to right*—Untreated control, 2.48, 0.982, 0.491, 0.246, and 0.123×10^{-2} M TIBA.

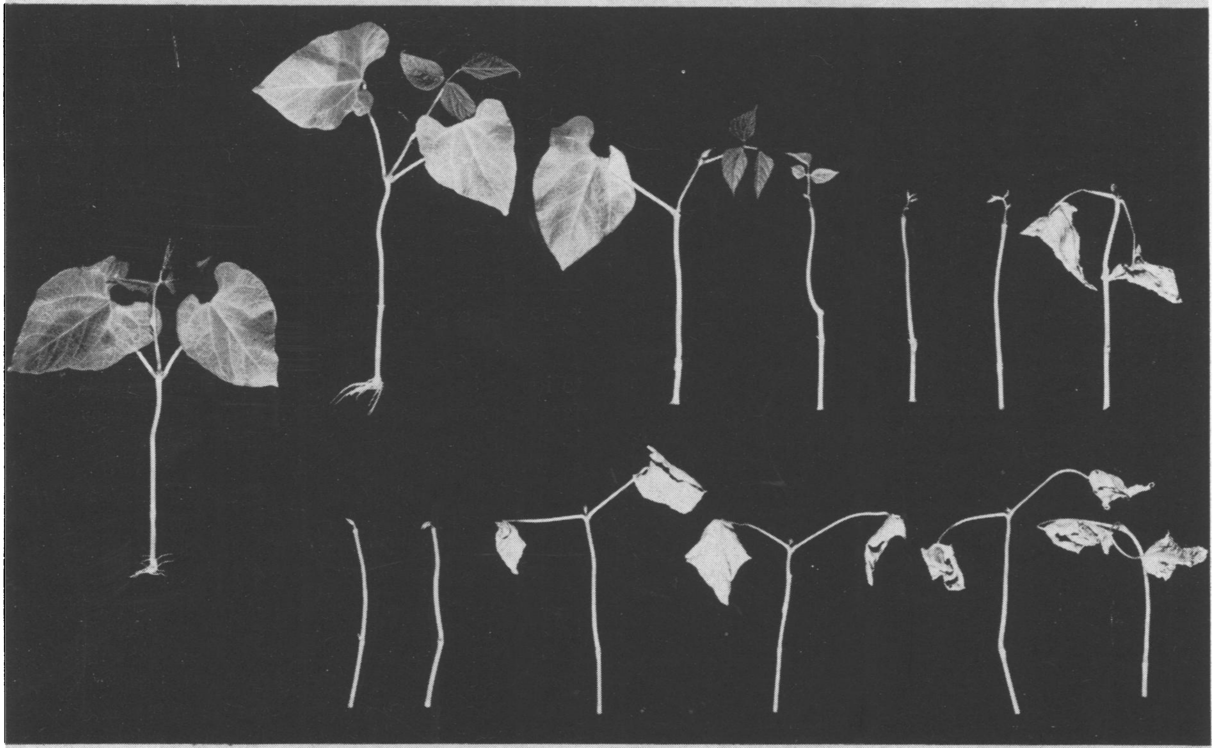

Table VII

Effect of Foliar Application of IAA Applied Simultaneously With KI to Tendergreen Beans*

Treatment	% Defoliation Days after treatment 3	6
KI & IAA (100 ppm)	0	17
KI & IAA (10 ppm)	44	44
KI	56	100
IAA (100 ppm)	0	0
IAA (10 ppm)	0	0

* Iodide concentration 2.94×10^{-2} M

the terminal meristem as growing points. To eliminate, as much as possible, all aerial meristemic growth, the primary terminal apex was cut off. The secondary buds were allowed to develop, then removed, and the plants were treated with KI. Table VI indicates nearly complete inhibition of defoliation when this procedure was followed. The normal desiccation associated with KI treatments was observed in the case of the decapitated plants, although abscission was nearly completely inhibited.

Previous workers have clearly established that indole-3-acetic acid (IAA) plays an important role in the control of abscission (1, 2, 3, 7, 11). Both promotive and inhibitory effects have been observed. The influence of IAA on iodide-induced defoliation was observed by application of the compound (10 & 100 ppm) as a foliar spray at the time of spraying the KI (iodide conc 2.94×10^{-2} M). It is apparent (table VII) that exogenous IAA inhibits the defoliation properties of the iodide ion when applied to the leaves only.

Table VIII

Effect of Photoperiod on Iodide-Induced Abscission

Iodide conc ($\times 10^{-2}$ M)	% Defoliation Days after treatment: 3 Photoperiod 8 hr	3 Photoperiod 16 hr	5 Photoperiod 8 hr	5 Photoperiod 16 hr	7 Photoperiod 8 hr	7 Photoperiod 16 hr
7.35	0**	0***	0	0	0	22
2.94	0***	50	5	88	15	100
1.47	83	55	100	88	100	100
0.74	83	0	100	72	100	77

** Complete death of the plants.
*** Nearly complete death of the plants.

Photoperiod is also known to influence abscission of plants (9). To determine if photoperiod affects the degree of defoliation observed with KI, Tendergreen beans were grown under 8- and the standard 16-hour photoperiods. The activity of the iodide was much greater in plants grown under 8-hour photoperiods than under 16-hour photoperiods (table VIII).

Susceptibility to iodide-induced abscission varies widely among different species and even between varieties of the same species (table IX). In other tests, cotton showed extremely high resistance to iodide-induced defoliation; approximately 1,000 times as much KI was required to defoliate immature cotton compared to the amount necessary to defoliate Tendergreen beans when applied to the soil. On the other hand, Coleus had approximately the same sensitivity as Tendergreen beans.

The stage of growth at the time of application will influence slightly the plant's degree of susceptibility

Table IX

Effect of KI on Abscission of Primary Leaves of Special Bean Varieties

Variety	% Defoliation Iodide conc ($\times 10^{-2}$ M) 7.35	2.94	1.47	0.74
Tendergreen	28*	39*	87	100
Black Valentine	11*	88*	100	89
Bountiful	11*	44*	87	89
French Horticulture	60*	44*	85	56
Pinto	0	0	0	0
Baby Lima	0	0	0	0

* Leaves severely desiccated and frozen on the stem.

to iodide-induced defoliation. Table X indicates this factor is not great, however. This also illustrates the iodide ion will induce abscission of trifoliate leaves as well as primary leaves.

Defoliation has been reported with 2,3,5-triiodobenzoic acid (TIBA) (12). A comparative test with KI and TIBA indicates the response induced by the latter compound (fig 3) was completely different from that observed with KI (fig 1). The iodide ion caused abscission of leaves present at the time of application leaving the new growth at the terminal apex relatively free from injury (unless excessive concentrations were used). TIBA, on the other hand, did not defoliate the primary leaves present at the time of application but caused abscission of the terminal apex and of all expanding trifoliate leaves.

Table X

Abscission of Leaves of Tendergreen Beans Treated at Various Stages of Growth With KI

Stage of development	% Defoliation Iodide conc ($\times 10^{-2}$ M) 5.65	2.26	1.13	0.57
10-day old, primary leaf expanded	100	100	89	78
15-day old, 1st trifoliate leaf expanded	44	100	100	...
35-day old, open flower	30	75	90	15
42-day old, mature fruit	0	70	90	80

Discussion

The iodide ion, either as an inorganic salt or organic complex, is the only halide which promotes abscission of Tendergreen bean leaves at the concentrations tested. This effect can be attributed to the iodide ion alone, although some effect of the cation was observed and is further substantiated by the ability of elemental iodine to induce abscission (8). The nature of this abscission is very different from that induced by TIBA, an organic iodine-containing compound.

That the cation exerts an influence on the rate and percentage of iodide-induced defoliation is evident. It is known that a deficiency of certain cations will induce premature leaf abscission. For example, suboptimal amounts of calcium, magnesium, and zinc induce premature abscission of citrus leaves (5). However, calcium was the only cation which reduced abscission induced by the iodide ion. There was no apparent pattern associated with the cation and further work will be required to clarify this point.

It is reasonable to suppose that transport of the iodide ion is by means of the xylem. This hypothesis is supported by observed movement of the ion from the roots to aerial portions of the plant. On the other hand, because the treated leaf of single leaf treatments was the only one to abscise, it is concluded that little or no movement occurred out of the treated leaf through the phloem. A concentration of the iodide ion sufficient to cause defoliation does not affect adversely the expanding trifoliate leaf. This may be considered to be due to the lack of phloem movement, or a consequence of biochemical retention of the iodide ion within the treated leaf.

Iodide appears able to induce leaf abscission rather generally among plants. Abscission has been induced in several different varieties of beans, Coleus (experiments not reported here show Coleus has approximately the same sensitivity to iodide-induced abscission as Tendergreen beans), and cotton. However, the degree of this response varies greatly. Immature cotton, for example, requires approximately 1,000 times as much of the iodide ion as the sensitive Tendergreen beans. The reason(s) for this difference is not known.

Although efforts were made to maintain uniform light intensities throughout, intensities under greenhouse conditions were variable. Lane and Hall (6) have shown light intensity to be important in chemical defoliation. The differences in the degree of susceptibility to iodide-induced defoliation (tables II & IV) could, in part, reflect differences in light intensity.

There are numerous indications of the role which IAA plays in leaf abscission. Probably the most widely accepted hypothesis is that of the auxin gradient (2) which requires a reduction in the amount of IAA in the leaf while the concentration in the stem remains relatively high. Although this work does not add any direct support, several points can be considered as indirect evidence for this hypothesis. The active meristem could be supplying necessary IAA to the stem. Elimination of this source of IAA either by physical decapitation or by rapid killing through excessive concentrations of the iodide ion, would account for the observed inhibition of abscission. The inhibitory influence of abscission by exogenously applied IAA to the leaves would also support this viewpoint. Hence, in the intact plant with an active meristem, it might be hypothesized that the iodide ion was inducing abscission by increasing, either directly or indirectly, the decomposition of IAA within the leaf, or by interfering in the normal biosynthesis of IAA. In either case there would be a net reduction of IAA within the leaf, as in the situation observed in bean leaves treated with the defoliant, NH_4SCN (10), while the IAA content in the stem was maintained. This would give rise to the auxin gradient hypothesized as necessary for leaf abscission. Studies to determine how the iodide ion induces abscission are currently in progress and will be the subject of subsequent communications.

Summary

The iodide ion is capable of inducing premature leaf abscission of intact plants. Although plants differ in their sensitivity to this phenomenon, it appears to be of general nature. An intimate relationship between iodide-induced abscission and IAA level also has been suggested.

Literature Cited

1. Addicott, F. T. & R. S. Lynch. 1951. Acceleration & retardation of abscission by indoleacetic acid. Science 114: 688–689.
2. Addicott, F. T. & R. S. Lynch. 1955. Physiology of abscission. Ann. Rev. Plant Physiol. 6: 211–238.
3. Biggs, R. H. & A. C. Leopold. 1957. Factors influencing abscission. Plant Physiol. 32: 626–632.
4. Boyd, L. Q. 1955. U.S. Patent No. 2,726,149.
5. Chapman, H. D. & W. P. Kelley. 1958. In: The Citrus Industry. I:719–766. H. J. Webber, & L. D. Batchelor, eds. University of California Press, Berkeley. 1028 pp.
6. Lane, H. C. & W. C. Hall. 1952. The effect of applied sugars, light intensity, & temperature upon the chemical defoliation of cotton. Science 116: 427–428.
7. LaRue, C. D. 1936. The effect of auxin on the abscission of petioles. Proc. Nat. Acad. Sci. U.S. 22: 254–259.
8. Nolan, J. H. 1960. U.S. Patent No. 2,937,081.
9. Olmsted, C. E. 1951. Experiments on photoperiodism, dormancy, & leaf age & abscission in sugar maple. Botan. Gaz. 112: 365–393.
10. Swets, W. A. & F. T. Addicott. 1955. Experiments on the physiology of defoliation. Am. Soc. Hort. Sci. 65: 291.
11. Wetmore, R. H. & W. P. Jacobs. 1953. Studies on abscission. The inhibiting effect of auxin. Am. J. Botany 40: 272–276.
12. Whiting, A. G. & M. Murray. 1948. Abscission & other responses induced by 2,3,5-triiodobenzoic acid. Botan. Gaz. 109: 447–473.