SUSCEPTIBILITY OF SEVENTY SPECIES OF FLOWERING PLANTS TO X-RADIATION

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(WITH FOUR FIGURES)

Introduction

Ten years of study of the effects of x-rays on different species of flowering plants has resulted in a grouping according to ray susceptibility which should be of value, since many investigators are engaged in studying the various ways in which radiation influences living organisms. When sufficient data concerning the morphological and physiological action of x-rays have been collected, it should be possible to give reasons for the ray resistance of some families as compared with the ray susceptibility of others. This paper deals particularly with the morphological effects produced on the above-ground parts of seventy different species distributed in thirty-five families; another paper (**11**) will discuss the action of the rays on underground stems or roots of twenty-two species. The susceptibility of species of *Helianthus, Solanum, Lycopersicum, Vicia, Atriplex, Linum, Nemophila,* and *Zinnia* have been treated elsewhere (**5, 6, 7, 8, 9, 10, 12**).

Methods

Seedlings were irradiated when the cotyledons were expanded and the growing tip visible. Pots or flats containing irradiated plants and controls were kept side by side on the greenhouse benches, so that all plants were exposed to the same environmental conditions except for the treatment. If the experimental plants were transplanted, the controls were also. Considerable preliminary work was carried on which is not here recorded. Some species were tested which failed to grow normally under greenhouse conditions or which gave such erratic results that the experiment seemed to be of little value. In many cases only one study was made of the species in question, but, with some in which results appeared to be contradictory, experiments were repeated many times.

Data on vegetative growth and blossoming were taken when most of the control plants had completed their growth. The facts set down for each species depended somewhat on the general form of the plant. In all cases the following were recorded: number of plants reaching maturity, age when irradiated, x-ray dose, and total height at maturity. The age in days refers to the number of days from the date of planting. The total height was recorded in all cases as the distance from the soil surface to highest point of the plant. In some cases this meant to the tip of the inflorescence, or, if the plants were still vegetative, to the tip of the highest leaf. In many cases the

age in days when the first blossoms appeared is given. Blank spaces in the columns of the table, where blossoming is considered, indicate a lack of first records of blossoming rather than an absence of flowering. If the plants were branched, records were taken which best indicated how branching was influenced by the radiation, such as percentage bearing laterals, average number of branches, and average length of branches.

In recording the x-ray doses, the r-units are stated for the later ones studied, while the set-up of the machine is given for those treated before a dosimeter was available. Unfiltered rays were used in all cases.

Observations

The families with the species studied may be grouped into three divisions: (1) species apparently unaffected by treatment; (2) species slightly affected, perhaps for only a short time after irradiation; and (3) species noticeably affected by the rays. Those in the first group so nearly resembled the controls in their growth that figures are not given except in a few cases. Species placed in the second and third groups are treated in greater detail.

Group I. Species apparently unaffected by x-radiation

The species listed in this group were treated in the seedling stage when the first foliage leaves were beginning to appear. From one dozen to two dozen plants of each species were given what may be considered a medium dose, 80–90 K.V. 5 ma., distance from the target to the growing point 30 cm., for 22 minutes. The plants were watched during their growth for indications of change due to x-ray treatment. Dates of blossoming of both groups of plants were recorded and at maturity the average height and average number of branches were determined. In this group, the experimental plants so nearly resembled the controls that the complete data are not recorded. The species apparently unaffected by moderate exposure to x-radiation were:

Chenopodiaceae
Blitum capitatum
Amaranthaceae
Amaranthus tricolor
Aizoaceae
Mesembryanthemum crystallinum
Ranunculaceae
Nigella damascena
Papaveraceae
Eschscholtzia
Capparidaceae
Cleome pungens
Crassulaceae
Sedum coeruleum
Tropaeolaceae
Tropaeolum majus
Primulaceae
Anagallis grandiflora
Boraginaceae
Cynoglossum amabile

Scrophulariaceae
Torenia fournieri
Dipsaceae
Scabiosa caucasica
Carduaceae
Aster
Emilia flammea
Calendula officinalis

The controls and irradiated specimens listed showed little or no difference in average height of plants at maturity. In most cases the dates of blossoming were the same in both groups. If any of the usual leaf irregularities which accompany the application of x-rays were evident during the early stages, they disappeared long before the plants were mature.

Two of the species listed above need special mention, *Mesembryanthemum crystallinum,* the ice plant, and *Sedum coeruleum,* the stonecrop. A preliminary experiment with irradiated seedlings of the ice plant indicated that irradiation caused no visible change in this species. Later 57-day-old seedlings were treated with 2500 r-units. There were thirty-three controls and twenty-one experimental seedlings which lived to maturity. The irradiated plants showed a gain not only in height, but in average number of branches per plant, and average dry weight per plant. A third study of this species was made, since increase in growth due to radiation is too unusual to record without numerous tests. Of the 69-day-old seedlings given 2500 r-units, seventeen controls and fourteen treated plants lived to maturity. Careful measurements of this group showed in the experimental plants reduction in average height, in the number of plants bearing branches, and in the number of branches produced. The treated plants were later in blossoming, and their green weight at the close of the experiment showed 20 per cent. reduction. Thus, while irradiation produced no visible damaging effect upon this fleshy, thick leaved plant, it is evident that there was no increased growth due to irradiation.

A preliminary test of the stonecrop indicated that irradiation of the seedlings with a medium dose did not visibly affect the development or the blossoming. A second test involving 234 44-day-old seedlings resulted in a slight decrease in the average height of the treated plants and a considerable reduction in the average green weight per plant. The time of flowering was not influenced by the treatment.

These two species, ice plant and stonecrop, well illustrate that although there seem to be in some species no visible effects produced by the rays, there is usually a reduction in amount of plant tissue produced by the treated specimens, as may be demonstrated by a comparison of green weights.

Group II. Species slightly affected by x-radiation

Species listed in group II are those which in their earlier stages gave evidence of being ray-susceptible, but as the plants matured they showed

TABLE I

GROUP II. SPECIES SLIGHTLY AFFECTED

FAMILY AND SCIENTIFIC NAME	AGE WHEN IRRAD.	SET-UP FOR DOSE OR DOSE IN R-UNITS	NO. OF PLANTS	
			CONTROL	IRRAD.
	days			
Chenopodiaceae				
*Chenopodium album**	.....	84 K.V. 10 ma. 30 cm. 10 min.	33	35
*Spinacia oleracea**	11	91 K.V. 5 ma. 30 cm. 20 min.	20	24
Amaranthaceae				
Celosia argentea	54	86 K.V. 5 ma. 30 cm. 23 min.	16	15
Portulacaceae				
*Calandrinia grandiflora**	48	2500 r-units	8	11
Portulaca grandiflora	41	48 K.V. 5 ma. 30 cm. 17 min.	22	24
" "	27	48 K.V. 5 ma. 30 cm. 33 min.	19	21
Ranunculaceae				
Delphinium	27	87 K.V. 7½ ma. 30 cm. 22 min.	12	4
Brassicaceae				
*Cheiranthus**	15	2500 r-units	14	18
Iberis umbellata	74	2500 r-units	16	19
*Matthiola bicornis**	18	83 K.V. 5 ma. 30 cm. 22 min.	9	7
Violaceae				
Viola tricolor	23	85 K.V. 5 ma. 30 cm. 26 min.	25	31
Onagraceae				
Gaura lindheimeri	47	91 K.V. 5 ma. 30 cm. 20 min.	9	8
Umbelliferae				
Trachymene coerulea	24	87 K.V. 7½ ma. 30 cm. 22 min.	23	18
" "	21	88 K.V. 5 ma. 29 cm. 17 min.	9	12
Convolvulaceae				
*Convolvulus minor**	21	100 K.V. 7½ ma. 30 cm. 22 min.	11	22
*Quamoclit coccinea**	34	83 K.V. 5 ma. 30 cm. 23 min.	4	7
Rubiaceae				
*Asperula orientalis**	51	95 K.V. 7½ ma. 30 cm. 25 min.	11	9

* Leaf irregularities such as puckering, ligulate form, and mottling due to abnormal chlorophyll development were evident during early growth but disappeared before maturity.

TABLE I

BY MEDIUM DOSES OF X-RAYS

Difference in treated plants					General effects of radiation
Av. height at maturity	Percentage plants bearing laterals	Av. no. laterals per plant	Av. length of laterals per plant	Age when flowers first appeared	
% (av. wt.)	%	%	%	%	
− 6.4†	.....	.....	.....	.....	Greater development of secondary branches
+11.5	− 26.3	−10.1	.....	+0.9	
−38.8	.....	−30.8	+16.5	.....	Irradiated plants show shortened inflorescences
−25.0	.....	.....	.....	.....	Reduction in number of leaves per plant; 82% reduction in plants bearing flower stalks
.....	.....	Same	+21.9	.....	Increased length of branching gives appearance of increased vigor
+ 8.4	+172.3	.....	+90.0	+6.7	No injurious effect apparent
−13.8	None	+25	.....	.....	Retarded growth evident
− 6.0	+210.5	+34.6	.....	.....	Delay in blossoming and fruiting
− 7.8	.....	.....	.....	+1.3	Reduction in blossoming; two cases of dichotomous branching
− 1.2	.....	+73.9	.....	.....	Increase in development of lateral branches
+ .3	+ 12.9	+33.3	.....	.....	Decrease in green weight shown in later study
−22.2	.....	.....	.....	.....	
+ 7.5	..... (Terminal branches)	.....	.....	.....	Greater height probably due to greater development of terminal branches
− 3.4	+ 14.9	.....	.....	+ 3.4	
−26.7	.....	.....	.....	− .8	
− 7.2	.....	.....	.....	−5.3	
−19.6	− 18.5	+11.7	− 7.9	.....	

† In this and other tables in this paper, the minus sign indicates that the treated plants showed less growth than the controls; the plus sign that the treated plants exhibited greater growth.

TABLE II

GROUP III. SPECIES NOTICEABLY

FAMILY AND SCIENTIFIC NAME	AGE IN DAYS WHEN IRRAD.	SET-UP FOR DOSE OR DOSE IN R-UNITS	NO. OF PLANTS	
			CONTROL	IRRAD.
Nyctaginaceae				
Abronia umbellata	44	2500 r-units	4	5
Caryophyllaceae				
Dianthus chinensis	21	51 K.V. 7½ ma. 30 cm. 22 min.	21	26
" "	49	2500 r-units	8	14
Gypsophila elegans	19	50 K.V. 5 ma. 30 cm. 22 min.	18	25
Lychnis coeli-rosa	20	44 K.V. 5 ma. 30 cm. 20 min.	14	49
Lychnis viscaria	43	53 K.V. 5 ma. 30 cm. 37 min.	30	30
Saponaria vaccaria	8	57 K.V. 7½ ma. 30 cm. 22 min.	11	17
Silene armeria	44	2500 r-units	47	71
Euphobiaceae				
Euphorbia marginata	44	2500 r-units	6	5
Ricinus communis	.....	3500 r-units	12	11
Balsaminaceae				
Impatiens balsamina	12	50 K.V. 7½ ma. 30 cm. 22 min.	24	45
Malvaceae				
Lavatera splendens rosea	19	85 K.V. 5 ma. 30 cm. 33 min.	11	15
Onagraceae				
Clarkia elegans	27	89 K.V. 5 ma. 35 cm. 20 min.	23	16
" "	27	1370 r-units	12	13
" "	27	3750 r-units	28	8
Godetia amoena	20	95 K.V. 5 ma. 30 cm. 23 min.	6	5

TABLE II

AFFECTED BY X-RADIATION

Difference in treated plants					General effects of radiation
Av. height at maturity	Percentage plants bearing laterals	Av. no. laterals per plant	Av. length of laterals per plant	Age when flowers first appeared	
%	%	%	%	%	
− 50.7	− 73.3	− 66.6	.....	+ 5.0	73.3% reduction in number of flower clusters; 70% reduction in green weight of above-ground parts
+ 4.5	+ 61.7	+ 107.9	.....	+ 6.3	Branching greatly increased
− 7.1	.....	− 34.0	.....	− 12.4	16% reduction in green weight; 12% increase in flower and bud production
− 16.5	.....	.....	.....	.....	Retarded growth; persistent leaf deformities
+ 7.1	− 5.1	Same	+ 125.3	.....	Increase in average length of main branches per plant
− 21.9	+ 13.4	+ 63.6	− 11.1	.....	Increase in number of lateral branches though not in average length
	(Terminal pedicel)	(Pedicels)	.....	.....	
+ 13.9	+ 10.1	+ 46.7	.....	− 4.0	Increased height due to greater development of terminal pedicels
− 7.3	+ 8.5	+ 33.3	.....	+ 2.7	
− 24.1	.....	.....	.....	.....	Leaf deformities conspicuous at maturity; little difference in time of blossoming
− 18.9	None	− 21.3	.....	.....	58% decrease in height to first branch
− 5.0	+ 216.7	+ 237.6	.....	+ 5.3	Considerable increase in lateral branching; some dichotomous branching
− 14.8	.....	.....	.....	.....	70% reduction in leaves at maturity; many deformed leaves present
+ 9.7	+ 140.0	+ 103.8	.....	+ 1.6	Increased number of lateral branches
+ 77.2	.....	+ 10.8	− 1.3	.....	
+ 13.6	.....	+ 45.4	+ 103.5	.....	Most of irradiated plants died before reaching maturity; resistant ones grew to great size
− 2.8	+ 200.3	+ 800.0	+ 706.0	+ 7.5	Leaves twisted and drawn to one side

TABLE II—(*Continued*)

GROUP III. SPECIES NOTICEABLY

FAMILY AND SCIENTIFIC NAME	AGE IN DAYS WHEN IRRAD.	SET-UP FOR DOSE OR DOSE IN R-UNITS	NO. OF PLANTS	
			CONTROL	IRRAD.
Convolvulaceae				
Ipomoea	44	2500 r-units	8	11
Polemoniaceae				
Cobaea scandens	22	92 K.V. 7½ ma. 30 cm. 23 min.	6	10
" "	19	93 K.V. 5 ma. 30 cm. 33 min.	6	6
Gilia	18	45 K.V. 5 ma. 30 cm. 22 min.	18	23
Hydrophyllaceae				
Phacelia campanularia	55	2500 r-units	4	4
Phacelia whitlavia	30	2500 r-units	46	37
Solanaceae				
Browallia elata	39	96 K.V. 5 ma. 30 cm. 23 min.	41	51
" "	52	3600 r-units	31	23
Nicotiana affinis	48	2500 r-units	7	7
Schizanthus wisetonensis	23	95 K.V. 5 ma. 30 cm. 18 min.	28	27
Salpiglossis sinuata	55	2500 r-units	3	5
Scrophulariaceae				
Alonsa linearis	30	48 K.V. 5 ma. 30 cm. 22 min.	22	16
" "	28	2750 r-units	25	24
Antirrhinum majus	52	2500 r-units	20	23
Linaria maroccana	37	105 K.V. 5 ma. 30 cm. 12.2 min.	16	5
Mimulus tigrinus	62	2000 r-units	8	8

TABLE II—(*Continued*)

AFFECTED BY X-RADIATION

Difference in treated plants					General effects of radiation
Av. height at maturity	Percentage plants bearing laterals	Av. no. laterals per plant	Av. length of laterals per plant	Age when flowers first appeared	
%	%	%	%	%	
−48.0	+ 63.6	+180.0	+200.0	+20.2	Leaves showed deformities, light areas, etc., even at maturity; 38% reduction in reproductive structures at conclusion of experiment
−30.4	.....	.....	.....	.....	Leaf deformities and reduced growth
−63.6	.....	.....	.....	.....	Leaf deformities still show at maturity
− 8.7	+ 14.6	+ 5.9	+ 35.2	+ 4.5	Greater development of lateral branches
		(Main branches)			2.8% increase in subordinate branches
+49.5	.....	− 25.9	− 14.1	.....	2.5% increase in average green weight per plant
					50% decrease in average number of flowers per plant
+10.6	+ 99.0	+ 72.7	.....	.....	Leaves of irradiated plants showed prominent white streaks; greatly increased branching
+ 5.3	− 23.1	−154.0	.....	+ 7.6	
−78.5	.....	.....	.....	.....	Blossoms never appeared, even after 122 days when controls were fruiting; irradiated remained dwarfed
−29.4	.....	.....	.....	.....	Retarded growth; leaf deformities; reduced blossoming
−38.0	.....	.....	.....	+11.1	47% reduction in number of inflorescences; 25% reduction in length of inflorescences
− 7.5	.....	.....	.....	+16.2	Over 50% reduction in buds and flowers
+ 6.5	+ 37.4	+137.6	+141.1	−18.1	Some dichotomous branching
− 9.9	Each 100%	− 9.6	.....	.....	33% of irradiated plants showed dichotomous branching
−10.3	+ 20.5	+ 5.5	+ 8.2	.....	Increased branching; reduced height; leaves in early stages showed spotting and streaking
−30.8	− 80.0	.....	.....	.....	Great increase in number of main branches from the base; fasciation in one central stalk
−31.7	.....	− 22.2	.....	.....	Reduced height; flowers of irradiated plants appear lighter in color

TABLE II—(*Continued*)

GROUP III. SPECIES NOTICEABLY

FAMILY AND SCIENTIFIC NAME	AGE IN DAYS WHEN IRRAD.	SET-UP FOR DOSE OR DOSE IN R-UNITS	NO. OF PLANTS	
			CONTROL	IRRAD.
Scrophulariaceae				
Nemesia versicolor	14	57 K. V. 7½ ma. 30 cm. 23 min.	5	18
Campanulaceae				
Campanula medium	47	2650 r-units	30	8
Valerianaceae				
Centranthus macrosiphon	44	2500 r-units	3	16
Carduaceae				
Acroclinium roseum	20	100 K.V. 5 ma. 30 cm. 23 min.	16	11
" "	27	3000 r-units	15	12
Arctosis stoechadifolia	29	50 K.V. 5 ma. 30 cm. 22 min.	10	16
Brachycome iberidifolia	44	2500 r-units	54	85
Dimorphotheca aurantiaca	22	93 K.V. 5 ma. 30 cm. 25 min.	12	5
" "	12	2500 r-units	24	29
Leptosyne stillmanii	8	91 K.V. 7½ ma. 30 cm. 22 min.	12	11
Rhodanthe manglesii	26	90 K.V. 5 ma. 29 cm. 17 min.	58	41
Sanvitalia procumbens	48	2500 r-units	16	47
Cichoriaceae				
Centaurea americana	49	2500 r-units	5	2

TABLE II—(*Continued*)

AFFECTED BY X-RADIATION

Difference in treated plants					General effects of radiation
Av. height at maturity	Percentage plants bearing laterals	Av. no. laterals per plant	Av. length of laterals per plant	Age when flowers first appeared	
%	%	%	%	%	
−12.4	− 7.5	− 6.2	.....	− 2.4	Leaf irregularities, ligulate form, pebbly, etc.
−45.7	.....	.....	.....	.....	Dose lethal to many seedlings; at close of the experiments when many controls were blossoming, 15.5% more of irradiated than controls were still in rosette form. Average green weight of irradiated plants was 40% less than that of controls
−15.8	−62.4	−83.7	−80.3	− 2.5	Puckered leaves; irregular chlorophyll development
+11.2	.....	+39.0	.....	+15.0	Apparent increase in vegetative growth
−39.8	.....	+22.2	− 1.4	.....	Blossoming delayed; number of main branches increased
−11.6	−43.8	−15.0	.....	.....	Leaf irregularities; terminal as well as lateral growth checked
− 6.8	−14.0	−57.1	.....	+17.6	Blossoms decreased 65%; 43% decrease in green weight
+30.6	None	+ 4.2	.....	.....	Increased height and branching
+12.4	.....	−14.8	−12.5	.....	Some increase in average number of subordinate branches per plant, but 27% decrease in average length per plant
−28.4	.....	.....	.....	− 3.5	One case of dichotomous branching
−16.9	−26.7	−16.7	.....	+ 7.3	Reduction in total growth and branching
−34.8	− 5.1	−27.2	−50.0	− 4.6	33% reduction in average number of flowers; ligulate flowers interspersed among disk flowers
−10.6	.....	.....	.....	+10.8	Plants noticeably injured; deformed, discolored leaves; dichotomous branching from base

rather good recovery, so that at maturity it was difficult to judge results without careful measurements and calculation of the percentage difference in the treated plants. All measurements taken and counts made are available for comparisons, but only calculations of percentage differences in treated plants are given in tables I and II. In a few cases the number of plants grown to maturity falls below a dozen specimens because of difficulties encountered in growing some of these forms in the greenhouse. Since even a small number of plants may give some indication of the susceptibility of the species, results involving a relatively small number of specimens have been included, in a few cases, with the idea that the reader will accept the results for these few species as being preliminary in nature.

The age in days at the time of irradiation necessarily shows considerable variation in range because of differences in germination and growth response of the various species. Treatment was given when the true foliage leaves were just beginning their development.

The following species in this group during early growth showed irregularities in the first few leaves which developed after radiation: *Chenopodium album, Spinacia oleracea, Calandrinia grandiflora, Cheiranthus, Matthiola bicornis, Quamoclit coccinea,* and *Asperula orientalis.* In some cases the leaves were deformed, puckered, and twisted to one side; in others a greater or less degree of mottling indicated some disturbance in chlorophyll development.

Particular attention is called to certain points indicated in table I. *Spinacia* and *Portulaca* are the only species which showed an increase in the average height. Although *Trachymene* is listed as showing the irradiated plants with greater height, this is probably due to a better development of terminal branches rather than to the development of the central stalk. Three species, *Cheiranthus, Viola,* and *Portulaca,* had a greater percentage of irradiated specimens than controls bearing lateral branches. Experimental plants of *Delphinium, Cheiranthus, Matthiola,* and *Viola* showed an increase in average number of lateral branches per plant. This condition commonly accompanies x-radiation, as shown by ANCEL (**1**) and the writer (**5, 7, 9, 10**). In *Celosia argentea,* there occurred a reduced number of lateral branches, but an increase in their average length. In *Asperula orientalis,* on the other hand, while there was an increase in the average number of lateral branches there was a decrease in their average length. In general, it has been found (**7, 9, 12**) that irradiation causes a delay in the time of blossoming. Delay is not as apparent in this group as in the third group.

GROUP III. SPECIES NOTICEABLY AFFECTED BY X-RADIATION

The dose of 2500 r-units, which was used on most of the species listed, proved lethal to seedlings of *Nemophila insignis, Gaillardia picta,* and *Phlox*

drummondii. A study with *Nemophila,* where the effects of various doses were determined, is reported elsewhere (**12**).

Forms which showed effects of treatment during the early seedling stages, and which at maturity showed also changes such as difference in height, number, and length of branches, and unusual cases of dichotomous branching, are grouped together in table II. The same general plan was followed with these species as was used with those of the other group. In general, a medium dose depresses the total growth when height of the plant is used as an indicator of growth. Of the thirty-nine species listed, but nine of them showed any increase in the total height of the treated plants.

The experimental plants of *Dimorphotheca* and *Clarkia* showed increase in height in several experiments. With the former, although the experimental plants increased in average height, there was a slight decrease in green weight. In *Clarkia* the dose was lethal for a considerable number of plants, and those remaining proved to be exceptionally strong, vigorous plants. This may also have been true for treated plants of *Acroclinium, Phacelia,* and *Saponaria,* which gave significant increases in total height.

The studies of others (**2, 3, 4, 13, 14, 16, 17**) and former experiments by the writer (**5, 7, 9**) have demonstrated the tendency for leaves of x-rayed plants to exhibit irregularities in shape as well as a peculiar pebbly, blotched appearance of the blade. Species differ considerably with respect to the length of time that this effect is evident. Nearly all the plants listed in this group had leaf deformities in their early growth stages. Those species showing less conspicuous deformities include *Gilia, Alonsa, Browallia, Mimulus,* and *Rhodanthe.*

X-radiation of some species (**5, 7, 9, 10**) is commonly accompanied not only by an increase in the percentage of plants bearing laterals but also by an increase in the number and average length of lateral branches per plant. Some species which normally do not form lateral branches, after irradiation often show either dichotomous or lateral branching. In one-third of the species listed in table II, the irradiated plants showed an increase over the controls in the percentage of plants bearing lateral branches. The increased branching accompanying radiation was most noticeable in members of the Caryophyllaceae and in the genera *Impatiens, Clarkia, Godetia, Ipomoea, Gilia, Phacelia, Antirrhinum,* and *Acroclinium.*

The time of first appearance of flowers was delayed in all species of experimental plants except six. Dichotomous branching, so common in irradiated *Helianthus* and *Zinnia,* appeared also in *Impatiens, Alonsa, Centaurea,* and *Leptosyne.*

Dimorphotheca aurantiaca

The effect of treatment upon the cape marigold, *Dimorphotheca aurantiaca,* of the Carduaceae is discussed to illustrate the fact that not all plant

species react in exactly the same manner to radiation. This species appeared severely affected during its early stages of growth but treated plants later showed increased height over the controls. After a preliminary experiment had indicated the sensitivity of this species to x-radiation, two more groups of plants were grown in which the seedlings were given approximately 2500 r-units. The leaves showed the usual effects, for they were irregularly ligulate in shape and presented the characteristic pitted, blotched appearance. The total height of the first group was increased 30.6 per cent. but there was little difference in the number of branches or in the time of blossoming. The increase in height was such an unusual response to radiation that a larger group of plants was grown and more complete measurements were taken.

Table II gives the percentage differences between the growth of control seedlings and those given 2500 r-units when twelve days old. In this group, growth of the treated seedlings was retarded for a time but at the age of five months, when the experiment was concluded, the average height of the central stalk was somewhat greater in the treated plants. The number of main lateral branches in the treated plants was decreased; in the subordinate branches, which developed later, the number was increased 9 per cent. but their average length per plant decreased 27 per cent. The average green weight of the treated plants, however, was 5 per cent. less than that of the controls, indicating that although these plants appeared to show increased size, there really was no actual increase in amount of plant tissue produced.

Counts of the number of faded blossoms as well as of the fresh flowers and buds were made at the conclusion of the experiment. Calculations of the percentage of the total number which were living at the end of five months showed 37 per cent. decrease on the main lateral branches of irradiated plants, but 228 per cent. increase on the central stalk, and a slight increase in the number of those on the subordinate branches. The greater percentage of living flowers and buds was present on the more recent vegetative growth of the treated plants because in the controls more of the flowers were older and had faded. The retarded vegetative growth was thus accompanied by delayed flowering.

This species does not show injury due to irradiation as clearly as do many of the composites. Although growth is retarded during the earlier stages, the experimental plants attained to as great or greater height than did the controls. The average green weight of the treated plants, however, was slightly less than that of the controls. The number of branches was in general decreased. The number of flowers produced was little affected by treatment, although the irradiated plants showed a greater number of living flowers at the close of the experiment because of the fading of the early flowers of the control.

Linaria maroccana

Linaria maroccana of the Scrophulariaceae showed a noticeable increase in the number of main branches from the base other than from the central stalk. This is a good example of a plant which from the first had difficulty in recovering from the x-ray dose. Although the leaves showed little effect, the stems were weak and decumbent, and at an early date an increase in branching was apparent. Growth habits in the treated plants were considerably altered. They had a thickened, twisted, hypocotyl region, and little distinction between main and secondary stalks. Table II shows the reduced height and decrease in lateral branches in the rayed plants. No flowers developed in the treated plants.

Campanula medium

Campanula medium seedlings showed a heavy mortality when given 2650 r-units. Of those which survived, 15 per cent. more of the irradiated than

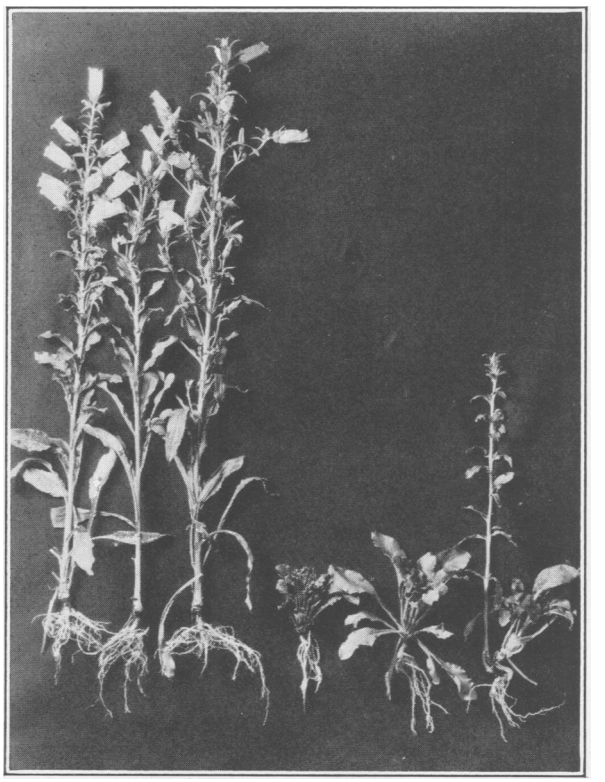

FIG. 1. *Campanula medium* plants 7 months old: Left, controls; right, plants irradiated with 2650 r-units. Plants which survived the dose showed greatly reduced height and weight. None of treated plants had blossomed at conclusion of experiment.

controls were still in the rosette stage when 208 days old. The controls were rather crowded, hence many remained in the rosette form that might otherwise have formed shoots. Table II records the lessened height and green weight of the treated plants. Figure 1 represents typical members of the control and treated groups at the close of the study. None of the experimental plants had blossomed at the conclusion of the experiment.

Salpiglossis sinuata

Salpiglossis sinuata proved to be ray susceptible as are many other members of the Solanaceae. Figure 2 represents the difference between irradiated

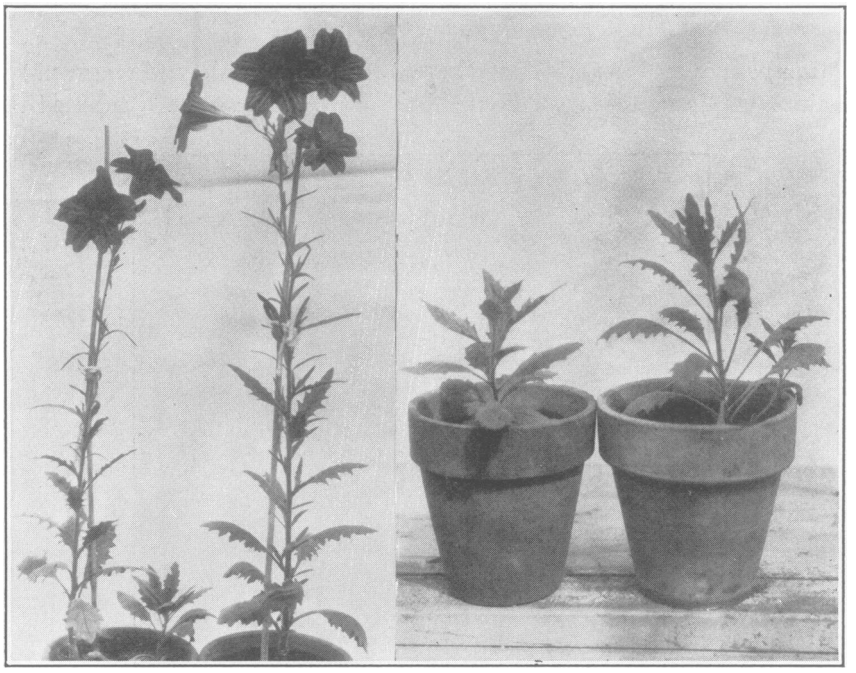

FIG. 2. *Salpiglossis sinuata* plants 160 days old: Left, controls; right, plants which received dose of 2500 r-units in seedling stage. When the photograph was taken, the average height of the irradiated plants was 57 per cent. less than that of the controls; the average number of buds and flowers was 5.3, while none had appeared in the treated plants.

and control plants when about five months old. Later, the irradiated plants showed more rapid growth so that when the records given in table II were taken, there was but 7.5 per cent. difference in average height between the control and the experimental plants. Flowering was greatly delayed and reduced in the treated plants.

Ricinus communis

Ricinus communis when irradiated with 3500 r-units showed reduction in average height due to a 58 per cent. decrease in average height to the first branch. This confirms the statement of RIVERA (**15**) that terminal shoot development of the castor bean is arrested by x-radiation. Figure 3, which

FIG. 3. *Ricinus communis* plants 8 months old: Left, controls; right, plants treated with 3500 r-units in seedling stage. The latter show reduced total height and increased branching. Most noticeable difference is 58 per cent. reduction in average height to first branch.

represents typical plants 222 days after treatment, shows the shortened stem below the branches as well as the reduced height. A mottled appearance of the leaves, decrease in average number of branches, and a reduction in number and length of roots are manifest in this species as in others.

DAY LENGTH AS INFLUENCING ACTION OF RAYS

The greater number of plants experimented upon were planted in the autumn, irradiated during the short days of winter, and records concerning total growth and branching were taken at maturity which occurred in the spring or early summer. Two species of plants, *Limonium sinuatum* and *Thunbergia alata,* which were irradiated during the long days of spring rather than during the short days of winter, gave unusual results which need special discussion.

Limonium sinuatum.—To determine whether *Limonium sinuatum,* a member of the Plumbaginaceae, was affected by the rays in a different way than are the majority of plants, it was grown three different years. Table III summarizes observations of inflorescence development of the members of the three groups. Seedlings of the first group, 18 days old, were irradiated in

TABLE III

EFFECT OF X-RADIATION UPON INFLORESCENCE DEVELOPMENT OF *LIMONIUM SINUATUM*

GROUP NO.	DATE OF TREATMENT	AGE IN DAYS WHEN IRRADIATED	DOSE	NO. OF PLANTS		DIFFERENCE IN TREATED PLANTS	
				CONTROL	IRRADIATED	AV. HEIGHT OF INFLORESCENCE	AV. NO. OF MAIN BRANCHES OF INFLORESCENCE
I	April 16	18	48 K.V. 5 ma. 30 cm. 33 min.	8	11	% None in irrad.	% None in irrad.
II	(1) Nov. 20	15	93 K.V. 5 ma. 30 cm. 23 min.	16	12	+ 3.5	+ 44.4
	(2) Dec. 13	38	90 K.V. 5 ma. 30 cm. 15 min.				
III	Dec. 6	24	80 K.V. 5 ma. 30 cm. 29½ min.	10	5*	− 1.0	+ 6.2

* During transplanting 50 per cent. of treated plants died.

April with one dose from the following set-up: 48 K.V. 5 ma. 30 cm. for 33 minutes. Eight months later when the study was concluded, 75 per cent. of the controls bore inflorescences while all the experimental plants remained in the vegetative stage. Leaves of the treated plants remained vegetative and were larger and more vigorous than those of the controls although there was little difference in the average number per plant. Roots of the control plants were long and spindling as compared with the short stocky growth in the other group.

The development of the inflorescences in the control and its absence in the irradiated plants constituted the most striking difference between the two groups. Because of the total absence of inflorescences in the treated group, other experiments were made to determine whether irradiation always prevented blossoming of members of this genus.

Seedlings of the second group which were irradiated in November were given two doses, the first from the set-up 93 K.V. 5 ma. 30 cm. for 23 minutes. After an interval of two weeks, a second dose of slightly less intensity was given. The irradiated plants were retarded in growth, had twisted and ligulate leaves, and, when at the age of four months the controls began to send up flowering stalks, the irradiated plants still remained in the vegetative

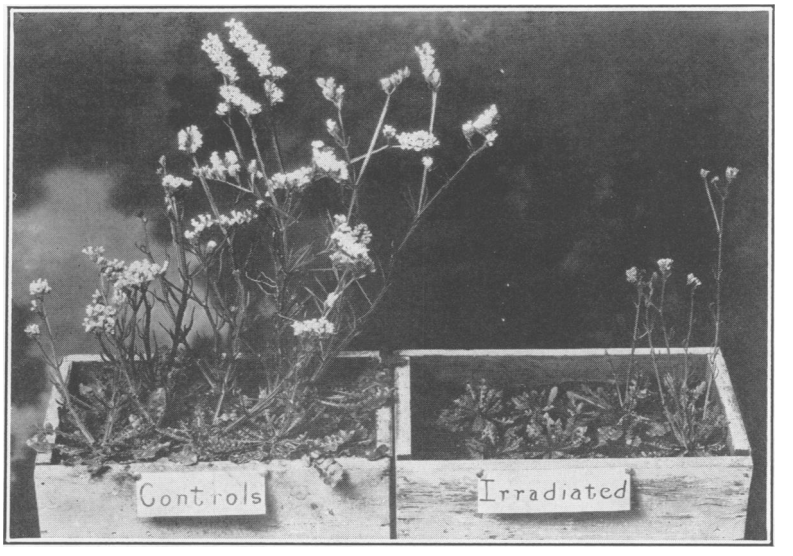

FIG. 4. *Limonium sinuatum* plants (group II) 6 months old. Seedlings of those at right were given two doses of approximately 1000 r-units in November. Note reduced vegetative and reproductive growth of treated plants. Plants of group I (not shown here) irradiated in April were still in rosette stage after 8 months; at this time, 75 per cent. of the controls bore inflorescences.

condition. Figure 4, taken at the age of six months, shows representative plants from both the control and irradiated groups. This experiment differs from the one previously described in that the vegetative and reproductive growth of the treated plants was greatly retarded, but flowering was not completely inhibited. Ten months after planting, the controls had all matured and were entirely dead while the green experimental plants showed stalks of the inflorescence which averaged as tall as those of the controls and they had 44 per cent. increase in the average number of flower stalks.

The following December, seedlings of another set, group III, were given one dose with the set-up 80 K.V. 5 ma. 30 cm. for 29½ minutes. Many of these died during transplanting, for their vitality seemed greatly lowered by the treatment. The vegetative portion of those remaining continued to be small and deformed but when the inflorescence finally developed, as many scapes were produced by the irradiated plants as by the controls and finally the branches of the inflorescence of the treated specimens attained practically the same height as the control plants.

Limonium which was irradiated during the fall reacted in about the same manner as other ray-sensitive species. The two groups of plants which were grown during the winter and spring developed normal inflorescences although they were considerably delayed. Plants germinated and irradiated in April, on the other hand, remained vegetative and at the end of eight

TABLE IV

EFFECTS OF X-RADIATION UPON *THUNBERGIA ALATA*

RECORDED DATA	GROUP I* (GROWN DURING SHORT DAYS)			GROUP II* (GROWN DURING LONG DAYS)		
	CONTROL	IRRADIATED 1280 R-UNITS	DIFFERENCE IN TREATED PLANTS	CONTROL	IRRADIATED 1320 R-UNITS	DIFFERENCE IN TREATED PLANTS
			%			%
No. of plants	15.0	12.0	.....	16.0	21.0	.....
Av. length of central stalk (cm.)	18.7	16.4	−12.3	10.7	9.9	− 7.5
Av. number of lateral branches per plant	3.5	2.7	−22.8	2.6	2.0	−23.1
Av. length of lateral branches (cm.)	25.0	12.2	−51.2	12.4	14.0	+12.9
Av. length of lateral branches per plant (cm.)	87.0	33.6	−61.4	32.5	28.7	−11.7
Av. time (days) before blossoming occurs (Data taken for each pot; not for each plant)	103.8	111.5	+ 7.41	94.4	100.5	+ 6.5

* Seeds for group I planted Nov. 5, 1931; seeds for group II planted Jan. 22, 1932.

months had not formed inflorescences. The controls blossomed at the usual time.

Thunbergia alata.—A member of the Acanthaceae, *Thunbergia alata,* showed greater injury to the vegetative growth and increased retardation in flowering when irradiation was given during the period of short days rather than when it occurred later in the spring. Seeds of group I were planted during the first week of November, and blossoming began the middle of February. Seeds of group II were planted the last of January, and blossoms first appeared the middle of April. The plants of group I were thus exposed to shorter days than were those of group II.

The leaves of all the experimental plants showed marked irregularities in shape, color, and size. Table IV indicates that length of central stalk, average length of lateral branches per plant, and average time before blossoming occurs, were very considerably reduced in all irradiated plants of both groups. Those planted and irradiated in the fall exhibited greater retardation in all these respects than did those planted and irradiated in the late winter and spring.

Discussion

The 15 species listed in group I (those apparently unaffected by x-rays) were judged chiefly by the presence or absence of leaf irregularities, average height at maturity, and time of blossoming—in other words, by visible symptoms. Had green and dry weight determinations been made, there is a possibility that all irradiated plants would have shown some reduced growth, for the stonecrop (*Sedum*) and ice plant (*Mesembryanthemum*), although manifesting no apparent injury, were found to have reduced green weight.

Difficulty arose in some cases in classifying plants with relation to x-ray susceptibility. Decision was based principally on the duration of leaf anomalies, if any occurred, as well as upon average height and branching. Other observers might have made somewhat different groupings.

Very few of the forty species listed among those which were noticeably affected developed any increase in total height of treated plants. In one-third of the group, among the irradiated there was a larger percentage of plants bearing lateral branches. Members of the Caryophyllaceae and Onagraceae were thus influenced. Dichotomous branching, which occurs so frequently in irradiated sunflower and zinnia plants, appeared in a few other species, particularly among composites.

In the severely affected group the first appearance of flowers was delayed, and usually the percentage of plants bearing flowers was reduced.

Studies with plants such as the cape marigold (*Dimorphotheca*) show the necessity of repeating experiments and waiting until maturity before drawing conclusions. This species manifested remarkable ability to recover

from the effects of the rays. Although there were fewer main lateral branches produced, the subordinate branches were more numerous and of greater average length. The blossoming on the central stalk and on the subordinate branches was considerably delayed in the treated plants although it was not actually decreased.

Other plants cited, because of their response to treatment, include: *Linaria,* which showed notable increase in the number of main branches from the crown; *Campanula,* typical of those plants which when irradiated remain for a long time in the rosette stage; and *Ricinus,* in which the branching occurred very much nearer the base of the plant in treated specimens.

Opportunity to observe how length of day affected x-rayed plants was presented in the case of *Limonium sinuatum* and *Thunbergia alata.* Plants of the former species rayed in the spring remained vegetative and in the rosette stage for eight months, while controls blossomed as usual. Irradiation in autumn brought about delay in blossoming but not complete inhibition. *Thunbergia* treated in the autumn was much more severely affected than were seedlings of the same species irradiated in the spring. It is possible that all species may be more injured when their seedlings are treated during short days.

It is impossible at this time accurately to state reasons for resistance or susceptibility of certain species, but observations from the large number of species examined seem to establish the fact that members of Chenopodiaceae, Portulacaceae, and Brassicaceae are in general resistant. The following genera in widely separated families, suffered some change in growth form, but on the whole were not noticeably injured: *Impatiens, Clarkia, Godetia, Gilia, Alonsa, Antirrhinum, Phacelia,* and various members of the Caryophyllaceae. Members of Solanaceae, Scrophulariaceae, and Carduaceae were the most severely affected. Genera noticeably ray-susceptible are *Abronia, Ricinus, Lavatera, Ipomoea, Cobaea, Linaria, Campanula, Centranthus,* and *Thunbergia.*

Summary

1. The seventy species of flowering plants distributed in thirty-five families considered in this paper were grouped as follows: fifteen species apparently unaffected by the rays; fifteen slightly affected, particularly during their early growth stages; the remaining forty species noticeably affected.

2. Members of the Chenopodiaceae, Umbelliferae, and Brassicaceae often gave indications of injury soon after treatment but by the time maturity was reached, manifested little effect.

3. Plants noticeably injured by radiation were marked by decrease in total height; increased branching as in the Caryophyllaceae and Onagraceae; frequent occurrence of dichotomous branching, particularly in the Cardua-

ceae; irregularities in shape, margins, and chlorophyll development of the leaves; delayed and reduced blossoming.

4. Members of the Solanaceae, Scrophulariaceae, and Carduaceae were noticeably ray-susceptible, as were also the following genera in other families: *Abronia, Ricinus, Lavatera, Ipomoea, Cobaea, Linaria, Thunbergia, Campanula,* and *Centranthus.*

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LITERATURE CITED

1. ANCEL, SUZANNE. Sur un phénomène de psuedo-excitation déterminé par les rayons x sur les bourgeons dormants cotylédonaires de la lentille. Bull. Soc. France **72**: 1084–1088. 1925.
2. GOODSPEED, T. H. The effects of x-rays and radium on species of the genus *Nicotiana.* Jour. Hered. **20**: 243–260. 1929.
3. HASKINS, C. P., and MOORE, C. N. Growth modifications in citrus seedlings grown from x-rayed seed. Plant Physiol. **10**: 179–185. 1935.
4. HORLACHER, W. R., and KILLOUGH, D. T. Radiation-induced variation in cotton. Somatic changes induced in *Gossypium hirsutum* by x-raying seeds. Jour. Hered. **22**: 253–262. 1931.
5. JOHNSON, EDNA L. Effects of x-rays upon growth, development, and oxidizing enzymes of *Helianthus annuus.* Bot. Gaz. **82**: 373–402. 1926.
6. ———. Growth and germination of sunflowers as influenced by x-rays. Amer. Jour. Bot. **15**: 65–76. 1928.
7. ———. Effect of x-irradiation upon growth and reproduction of tomato. Plant Physiol. **6**: 685–694. 1931.
8. ———. On the alleged stimulating action of x-rays upon plants. Amer. Jour. Bot. **18**: 603–614. 1931.
9. ———. The influence of x-radiation on *Atriplex hortensis* L. New Phytol. **32**: 297–307. 1933.
10. ———. Growth forms of *Linum grandiflorum* changed by x-radiation. (Torreya). (Unpublished.)
11. ———. Development of roots and underground stems as influenced by x-radiation. Univ. Colorado Studies **23**: 1936.

12. ————————. The relation of x-ray dosage to degree of injury in *Nemophila* and *Zinnia*. Amer. Jour. Bot. (Unpublished.)
13. McKay, J. W., and Goodspeed, T. H. The effects of x-radiation on cotton. Science n.s. **71**: 644. 1930.
14. Morgan, W. P. Growth irregularities in hybrid freesias induced by x-rays. Indiana Acad. Sci. **41**: 139–144. 1932.
15. Rivera, V. Azione dei raggi Röntgen sopra meristemi normali di *Ricinus communis*. Boll. R. Staz. Pat. Veg. **6**: 144–152. 1926. (Biol. Abstr. **2**: 16126.)
16. Shull, C. A., and Mitchell, J. W. Stimulative effects of x-rays on plant growth. Plant Physiol. **8**: 287–296. 1933.
17. Sprague H. B., and Lenz, M. The effect of x-rays on potato tubers for "seed." Science n.s. **69**: 606. 1929.