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Comparative radiosensitivities of main and accessory buds of sweet cherry (*Prunus avium* L.) with different irradiation methods

[Radiosensitiviti perbandingan tunas utama dan aksesori ceri manis (*Prunus avium* L.) dengan beberapa kaedah sinaran]

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Key words: irradiation, main, accessory, LD50, aberrations

Abstrak

Untuk menentukan LD50, tunas utama dorman Napoleon yang telah didedahkan pada sinaran gama 4–12 kR secara akut atau berperingkat dibiarkan bertunas di dalam rumah kaca. Tunas aksesori yang tidak disinar dan yang disinar juga dibiarkan bertunas di rumah kaca. Untuk eksperimen di ladang, tunas utama dan tunas aksesori Bing pada skion yang dorman disinar dan kemudian dicantum. Kemandirian dan percambahan tunas primer (M1V1) diamati. Nilai LD50 untuk sinaran akut dan berperingkat di udara ialah 5.0 kR, 5.5 kR untuk sinaran akut di dalam air dan 6.0 kR untuk sinaran berperingkat di dalam air. Untuk eksperimen di ladang, LD50 tunas utama Bing ialah 3.5 kR untuk sinaran akut dan berperingkat di dalam udara. Di dalam air, LD50 ialah 5 kR untuk sinaran akut dan 6.5 kR untuk sinaran berperingkat. Antara tunas M1V1, 52% menunjukkan daun yang beraberasi dan 33% berdwicabang dan/atau gempal. Dalam eksperimen di ladang bagi tunas aksesori yang disinari, percambahan tunas dipengaruhi oleh dos sinaran, kematangan tunas mengikut kedudukannya di dahan, dan kesuburan dahan berdasarkan lilitannya. Pada keseluruhan perlakuan, bilangan mata tunas yang bercambah pada setiap tapak tunas berkurangan daripada pangkal ke hujung, berkurangan dengan dos yang meningkat, dan berkurangan pada sinaran akut berbanding dengan berperingkat. Enam belas peratus daripada bilangan tunas M1V1 hasil sinaran tunas aksesori mempunyai daun yang beraberasi, dua daun mutan keseluruhan dan dua mempunyai ruas yang pendek.

Abstract

For determination of LD50, dormant main buds of Napoleon exposed to 4–12 kR of acute and fractionated gamma rays were forced in the glasshouse. Forcing of unirradiated and irradiated accessory buds was also done in the glasshouse. For the field experiment, Bing main and accessory buds on dormant scions were irradiated and then grafted. Survival and growth of primary (M1V1) shoots were observed. The LD50 values were about 5.0 kR for both acute and fractionated irradiation in air, 5.5 kR for acute exposure in water and 6.0 kR for fractionated dose in water. In the Bing field experiment with main buds, the LD50 for both acute and fractionated irradiation in air was 3.5 kR. In water, the LD50 was 5 kR

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for acute treatment and 6.5 kR for fractionated dose. The M1V1 shoots showed 52% frequency of leaf aberrations, and 33% bifurcations and/or fasciations. In the irradiated accessory bud field experiment, bud growth was influenced by irradiation dosage, bud maturity as related to position on the scion, and vigor of scions as represented by diameter. With all treatments, the number of buds that grew per potential bud site decreased from the base towards the tip, decreased with increasing dosage, and decreased with acute as compared with fractionated irradiation. Sixteen per cent of the M1V1 shoots derived from accessory bud irradiation had aberrant leaves, two were total leaf mutants and two had shorter internodes.

Introduction

Exposure of dormant scions to acute and semi-acute gamma rays in air (Lapins 1965; Decourtye 1970; Poll 1974; Thompson 1979; Ikeda and Nishida 1982) or in water (Campbell and Lacey 1973; Lacey and Campbell 1977) has induced beneficial mutations in deciduous fruit trees. Irradiation at higher doses caused substantial cell elimination which led to a reduction in the number of initial cells as well as increases in the size of mutated sectors (Gaul 1961; Lacey and Campbell 1979) and mutation frequency (Lapins 1973; Zagaja et al. 1982). Lapins (1971) as well as Katagiri and Lapins (1974) reported that accessory buds of sweet cherry had fewer cells than the apical meristems of main lateral buds. In comparison with more developed main buds, accessory buds gave a higher proportion of total mutants in cherry (Lapins 1971), pear (Nishida 1973) and a higher frequency of growth-reduced mutants in apple (Zagaja and Przybyla 1973).

Although the mutation rate increases at higher doses, recovery of mutants may be lower due to excessive cell injury and death. Therefore, doses approximating LD50 (amount of energy required to produce 50% lethality) have been found to be most effective for useful mutation induction. Irradiation of dormant sweet cherry buds with acute gamma or X-rays at LD50 of 4–4.5 kR has been successful in inducing mutations, including compact growth mutants (Lapins 1963, 1971; Donini 1976; Thompson 1979). In apple, compact mutants have been induced at LD30 (Visser 1973) and LD50 (Lacey and Campbell 1982). To determine radiosensitivity and LD50, irradiated buds were forced in the greenhouse (De Vries et al. 1970; Donini 1974).

The experiments in this irradiation study of Napoleon and Bing sweet cherry (*Prunus avium* L.) aimed to determine LD50s for main and accessory buds with acute and fractionated irradiation in air and in water, to determine if irradiation of accessory buds would result in larger mutant sectors in V1 shoots than irradiation of main buds, and to identify the most appropriate developmental stage of accessory buds for successful forcing for mutation induction.

Materials and methods

Forcing of Napoleon main and accessory buds

For determination of the LD50 of Napoleon, lateral main buds were forced in the glasshouse in 1983. Dormant scions were collected in mid-January at the Lewis Brown Horticulture Farm, Oregon State University. The scionwood was stored at 0 °C before irradiation in early March. Fifteen 20 cm scions per treatment were placed with basal end up` in the high-flux irradiation chamber with a dose rate of 670 rad/min and exposures of 4–12 kR, acute or fractionated gamma rays, in air or in water at the Radiation Center ^{60}Co facility. Dose fractionation consisted of 1–2 kR exposures at 12-h intervals. Following irradiation, both treated and control scions were forced in the

glasshouse by submerging the basal 4 cm in water. The water was replaced twice a week and 1 cm of the submerged ends were cut back weekly. Growth and survival of the top 3–5 lateral buds on each scion were recorded weekly for 1 month.

Forcing of unirradiated Napoleon accessory buds in the glasshouse was also carried out in March 1983. All main lateral buds on 18–20 cm scions were excised by making *V* cuts at their bases, leaving two potential accessory bud sites at each node. Lanolin was applied on the cut surfaces, the basal 4 cm of the scions was immersed in water, and the containers were maintained in the glasshouse at 20 °C. The number of accessory buds that developed shoots was recorded 4 weeks later. The experiment was repeated in March 1984 with controls and also with accessory buds that had been exposed to 3, 4, 5 or 6 kR acute gamma rays in water.

Irradiation of Bing main and accessory buds for the field experiment

For the Bing main bud irradiation in 1983, dormant 1-year-old scions were obtained from a commercial nursery in mid-January and stored at 0 °C until irradiation on 16 April. The irradiation methodology and range of exposures (3–10.5 kR) were the same as that for the glasshouse experiment. The scions were then grafted into limbs of Mazzard seedling rootstocks. The number of primary or M1V1* shoots, length of shoots, and leaf and growth aberrations on shoots were recorded in August.

For the Bing accessory bud irradiation in 1984, dormant scions were obtained from a commercial nursery in late January. Also, V1 shoots derived from both irradiated main and accessory buds of Bing were collected in late February. The scions were held at 0 °C until irradiation on 20 April with 3 kR or 4 kR fractionated doses in water. All main buds were excised, and both treated and controls were then grafted in the field. Bud survival, length of shoots and leaf, and growth aberrations were recorded 9 weeks after grafting. To determine the effect of bud position on accessory bud development, another group of scions was cut into three 17 cm sections (minus the immature 10 cm tip) and labelled terminal (A), mid (B) and basal (C), and exposed to 3 kR or 4 kR acute in air or fractionated in water. Bud survival and diameter of scions of V1 shoots were recorded in mid-September.

The Chi-square test and SPSSX (Statistical Packages for Social Sciences, 1983) were used to compare the various treatments.

Results

Determination of LD50 for forced Napoleon main buds

The average bud survival for irradiated (4–6 kR) Napoleon scions forced in the glasshouse was significantly higher for exposures in water (61%) than in air (49%), but there was no significant difference between fractionated (58%) and acute (53%) irradiation *(Table 1).* LD50 values, based on survival of forced buds at the end of the third week, were about 5.0 kR for both acute and fractionated irradiation in air, 5.5 kR for acute exposure in water and 6.0 kR for fractionated dose in water. Six kR was the highest dosage of any treatment which resulted in viable shoots at 1 month. Even though attempts were made to force some buds from higher dosages (fractionated in both air and water, and acute in water), shoots failed to grow.

Forcing of unirradiated and irradiated Napoleon accessory buds in the glasshouse

In 1983, unirradiated Napoleon scions had an average of 0.39 accessory bud forced per site after 30 days in the glasshouse *(Table 2).* Of 75 nodes, 52% had single and 13% had double accessory buds forced. In the remaining 35% bud sites, no accessory buds forced. In 1984 controls, 0.69 accessory bud

*hereafter referred to as V1

Table 1. Survival and growth of irradiated main buds of Napoleon forced for 21 days in the greenhouse

Irradiation technique	Dose (kR)	Potential no. of buds	Bud survival		Shoot length	
			No.	%	cm	%[a]
Control						
Dormant buds	0	139	136	98	3.6	100
Irradiated in air						
Acute	4	67	44	66	2.1	58
	5	73	39	53	1.4	39
	6	71	17	24	0.9	25
Fractionated	4	70	50	71	2.3	64
	6	71	22	31	2.1	58
	8	67	9	13	d	d
Irradiated in water						
Acute	4	67	55	75	2.5	69
	5	68	41	60	1.3	36
	6	62	25	40	1.2	33
	8	70	14	20	wd	wd
	10	67	17	25	wd	wd
	12	69	6	9	wd	wd
Fractionated	4	62	50	81	2.8	78
	6	64	30	47	1.9	53
	8	66	21	32	wd	wd
	10	70	9	13	wd	wd
	12	64	4	6	wd	wd
Subtotal						
In air	4–6	352	172	49b	1.8	49
In water	4–6	323	201	61c	1.9	54
Acute	4–6	408	221	53b	1.6	44
Fractionated	4–6	267	152	58b	2.3	63

a = % of control; wd = wilted or dead
Mean values with different letters differ significantly at p = 5% using Chi-square test

Table 2. Number of accessory buds forced on unirradiated and irradiated dormant scions of Napoleon after 30 days in the glasshouse

Irradiation method	Dose (kR)	No. of scions	Potential bud sites	Buds forced per site	
				No.	% of control
1983					
Unirradiated	0	18	150	0.39	
1984					
Unirradiated	0	15	140	0.69	100
Acute in water	3	14	142	0.53	77
	4	14	146	0.21	30
	5	14	128	0.10	14
	6	14	140	0.12	17

Table 3. Bud survival of Bing V1 shoots derived from irradiated main buds: field experiment

Irradiation technique	Does (kR)	No. of scions	Total no. of buds	No. of survival buds
Control	(0)	21	59	47 (100)[a]
In air				
Acute	3	23	105	52 (63)
	4	46	175	32 (23)
	5	42	175	12 (9)
	6	23	99	0
Fractionated	4	23	99	29 (36)
	5	44	184	23 (16)
	6	49	185	16 (11)
	7	23	95	3 (4)
In water				
Acute	4.5	47	207	148 (90)
	5.5	47	178	38 (26)
	6.5	22	100	10 (13)
	8.5	23	100	1 (1)
Fractionated				
	4.5	23	94	76 (100)
	5.5	48	184	128 (88)
	6.5	46	203	75 (46)
	7.5	24	111	37 (41)
	10.5	23	91	11 (15)
Subtotal				
In air	(3–6)	250	1 022	164 (16)
In water	(4.5–6.5)	233	966	465 (48)
Acute	(3–6.5)	250	1 039	292 (28)
Fractionated	(4–6.5)	233	949	347 (37)

a = % of control

had forced per site in the glasshouse *(Table 2)*. A single accessory shoot grew at 43% of the nodes, double accessory buds developed at 47% of the nodes, and at the remaining 10% no accessory buds forced. The LD50 for forced accessory buds (i.e. in terms of 50% of the buds that forced in controls) following acute gamma irradiation in water was approximately 3.5 kR *(Table 2)*.

Irradiation of Bing main buds: field experiment

The LD50 for both acute and fractionated irradiation in air was approximately 3.5 kR *(Table 3)*. In water, the LD50 was 5 kR for acute treatment and 6.5 kR for fractionated dose. The main buds tolerated higher exposures in water than in air, and higher for fractionated than for acute irradiation. Of 691 buds on irradiated scions that showed initial growth, only 408 (59%) developed into shoots, the rest either formed rosettes or did not survive. With increasing doses, there was decreasing bud survival; acute treatments caused a more abrupt decline than fractionated.

Growth of V1 shoots from irradiated main buds was similar to that described by Pratt (1968) and Thompson (1979). The lower 10 leaves from irradiated buds exhibited radiation damage; the first 4–5 leaves were spaced closer, smaller, with irregular margins and small chlorotic spots, whereas the next 3–5 leaves were larger and tended to be asymmetrical. Above the 10th node, some leaves were aberrant or vestigial leaves. Some aberrant leaves represented mutations while others apparently were

Table 4. Growth and development of Bing V1 shoots derived from main buds: field experiment

Irradiation technique	Dose (kR)	No. V1 shoots	Av. length (cm)	Aberrant shoot		Bifurcation (%)	Rosettes (%)[b]
				No.	%		
Control	(0)	12	76 (100)[a]	0		0	0
In air							
Acute	3	33	57 (75)	14	42	12	35
	4	24	45 (60)	11	46	13	29
	5	4	21 (28)	1	25	0	60
	6	0	–	–		–	–
Fractionated	4	12	66 (87)	8	67	0	29
	5	17	68 (89)	10	59	6	23
	6	16	66 (87)	10	63	6	6
	7	2	–	1	–	1	
In water							
Acute	4.5	83	70 (92)	50	60	2	39
	5.5	34	64 (84)	13	38	18	21
	6.5	7	58 (77)	3	43	14	22
	8.5	1	–	1	–	–	
Fractionated							
	4.5	50	61 (80)	27	54	4	35
	5.5	62	72 (94)	37	60	10	46
	6.5	37	73 (97)	17	46	5	46
	7.5	22	72 (94)	10	45	0	39
	10.5	5	51 (67)	1	2	7	
Subtotal							
In air	(3-6)	108	54 (71)	54	50	8	30
In water	(4.5–6.5)	301	66 (87)	147	49	7	39
Acute	(3–6.5)	186	53 (70)	92	49	9	35
Fractionated	(4-6.5)	223	68 (89)	109	49	6	39

a = % of control; b = % based on (no. of V1 shoots + no. of rosettes)

caused by irradiation damage to the apical region. Shoots with disrupted phyllotaxy were frequently observed. The frequency of shoots with leaf aberrancies (aberrant shoots) above the 10th node in V1 shoots of Bing ranged from 25% to 67% depending on the dosage with the average frequency at 52% *(Table 4)*.

The aberrant leaf frequency ranged from 51% to 56% following exposures in air or water with acute or fractionated doses. No V1 shoots from irradiated main buds had all aberrant leaves, i.e. there were no total leaf mutants. There was 3% to 72% reduction in length of V1 shoots from irradiations. For all irradiation treatments, 15% of the shoots were bifurcated or fasciated. Of the total 409 irradiated nodes with surviving shoots, six (1.5%) had 2–3 multiple shoots arising at the bases of the nodes. No bifurcations, rosettes or multiple shoots were observed in controls.

Irradiation of Bing accessory buds: field experiment

In the 1984 irradiated Bing accessory bud field experiment, bud growth 2 months after grafting was influenced by irradiation dosage, bud maturity as related to position on the scion, and vigor of scions as represented by diameter. With all irradiated treatments, the number of buds that grew per potential bud site decreased from the base towards the tip, decreased with increasing dosage, and decreased with acute as compared with fractionation (*Table 5* and *Table 6*). In controls, the number of forced buds per site was 0.19 in (A), 0.37 in (B)

Table 5. Leaf and growth aberrations on Bing V1 accessory shoots following fractionated irradiation in water

Scion	Dose (kR)	No. of scions	No. of V1 shoots	Av. length (cm)	Aberrant shoots		Bifurcation (%)	Rosette (%)[a]
					No.	%		
Bing standard	0	10	25	68	0		16	19
	3	50	126	64	24	19	11	13
	4	50	91	64	14	15	10	7
Subtotal		100	217	64	38	18	11	10
VI Bing accessory	0	10	31	56	0		16	24
	3	50	107	57	15	14	19	28
	4	47	87	55	12	14	13	19
Subtotal		97	194	56	27	14	16	24
V1 Bing main	0	9	31	71	0		10	23
	3	22	66	63	9	14	20d	21b
	4	49	63	72	10	16	11d	11b
Subtotal		71	129	68	19	15	16	16
All scion types	0	29	87	65	0		14d	22
	3	122	299	61	48	16	17d	21b
	4	146	241	64	36	15	11d	12c
Total		268	540	63	84	16	14	17

a = % based on (no. of surviving shoots + no. of rosettes)
Mean values in each column and row with different letters differ significantly at $p = 0.01$ using Chi-square test

Table 6. Forcing of irradiated Bing accessory buds in relation to scion maturity dosage and irradiation technique (field experiment)

Irradiation technique	Scion maturity	Scion diameter (cm)	No. of buds forced per site at 3 dosages		
			0 kR	3 kR	4 kR
Acute in air	Termind	0.50–0.60 (A)	7 (0.19)	0	0
	Mid	0.61–0.80 (B)	30 (0.37)	9 (0.06)	1 (0.003)
	Basal	0.81–1.00 (C)	63 (0.48)	4 (0.33)	–
Fractionated in water	Termind	0.50–0.60 (A)	7 (0.19)	11 (0.10)	21 (0.09)
	Mid	0.61–0.80 (B)	30 (0.37)	193 (0.28)	166 (0.18)
	Basal	0.81–1.00 (C)	63 (0.48)	152 (0.43)	43 (0.32)

and 0.48 in (C). With 3 kR fractionated irradiation in water, the number of buds forced decreased to 0.1 in (A), 0.28 in (B) and 0.43 in (C), and with 3 kR acute irradiation in air, the number per site decreased further to 0 in (A), 0.06 in (B) and 0.33 in (C). At the higher acute dosage, 4 kR, virtually no accessory buds forced, whereas with this same dosage fractionated, there were 0.09 in (A), 0.18 in (B) and 0.32 in (C).

Since frequencies of accessory shoots with at least one aberrant leaf were not significantly different for the irradiated Bing standard and reirradiated (V1 accessory and V1 main), and with 3 kR and 4 kR fractionated doses in water, the data were pooled *(Table 5)*. Of 540 V1 shoots derived

from accessory buds, 84 (16%) had 1–30 aberrant leaves. The frequency of stem bifurcations in accessory buds was not related to irradiation dosage; there were 17% at 3 kR, 11% at 4 kR and 14% for control. The frequency of rosettes were similar in control (22%) and at 3 kR (21%), but was less at 4 kR (12%).

V1 shoots from irradiated buds had 4 (0.74%) total mutants, 2 with shorter internodes and 2 with total leaf mutants. Multiple shoots (3–5) regenerated on 15% of the irradiated nodes compared with 4% at control nodes.

Discussion

The greater tolerance of apical meristems to higher irradiation dosage in water than in air indicates that water slightly buffered tissues against radiation damage. Water provides a more even dose distribution by preventing `surface build-up', effect of gamma radiation (Lacey 1976; Lacey and Campbell 1979). `Direct hits' from exposures in air are more damaging to the cells.

With irradiation in water, the LD50s were the same for forced buds in the glasshouse and for grafted trees in the field, whereas for irradiation in air the LD50s in the glasshouse were 1.5 kR higher than in the field. The difference in LD50s for irradiation in air under the two environments reflects the length of time elapsed before evaluation. In the glasshouse, buds were evaluated at the third week and in the field, evaluation was done at the ninth week. In the field, although some buds pushed initially, they failed to continue growing.

In both the glasshouse and field experiments, the difference in radiosensitivities of main and accessory buds was reflected in lower LD50 for the latter. Katagiri and Lapins (1974) reported that accessory buds of Bing cherry were more radiosensitive than the apical meristem of main buds because they are less advanced ontogenetically and, thus, have fewer meristematic cells. Because there are fewer apical initials in accessory buds and less intrasomatic competition, there should be a greater chance of recovery of total shoot mutants. Four (2 leaf mutants and 2 compacts) V1 accessory shoots were total mutants, but there were none in shoots derived from main buds.

Along a scion shoot, dormant accessory buds were at various stages of development as indicated by the decreasing percentage of buds forced from the base to the top. Lapins (1971) reported that 30% of the accessory bud sites in dormant buds of Bing had developed bud initials with meristematic tissues of 150–450 μ in width. Katagiri and Lapins (1974) observed that removal of the main buds forced accessory buds to produce shoots, but did not stimulate accessory buds at sites where bud initials had not yet developed. As the stage of development is related to age of the node and vigor of the shoot, we obtained the highest percentage of forced buds from the basal portion of vigorous shoots.

Moderate irradiation damage to the promeristem of the shoot apex and recovery by flank meristem has been reported to cause bifurcated shoots (Lapins and Hough 1970). We observed the highest frequency of bifurcations (18%) for acute 5.5 kR irradiation in water. Lapins et al. (1969) reported that for apple the highest frequency of bifurcations was 57% at 3.5 kR and for peach it was 18% at 5 kR. Bishop (1967) observed up to 30% bifurcations in shoots of irradiated apple scions, whereas the control had less than 1%. He suggested that the bifurcations were due to an upset in the polarity of meristematic divisions caused by the irradiation.

Severe damage to the apical meristem of main buds frequently caused rosetting (35% of all irradiated buds vs. none in controls). In rosettes, only the preformed leaf primordia developed into highly aberrant tightly spaced leaves. A less frequent consequence of apical meristem damage is the formation of multiple shoots at a node (2% in main buds vs. none in controls). Possibly this is due to forcing of lateral meristems.

The much higher frequency of multiple shoots at irradiated accessory bud sites (15%) compared with main bud sites (2%) can be explained by the differential effect of irradiation on the two developmental stages. Scattered cell damage, as reported by Pratt (1968), is not sufficient to totally disrupt the integrity of the more highly developed, multicellular, apical meristem of the main bud. However, scattered as well as localized cell damage (Saamin and Thompson 1989) in the less developed accessory bud meristems could cause lesions between the relatively few cells, and thereby stimulate the organization of as many apices as there were lesions. The relatively few multiple shoots at non-irradiated accessory nodes (7%) may have been induced by physical damage or shock due to excision of the main bud. Comparable frequencies of bifurcations and rosettes in irradiated and non-irradiated buds suggest that these responses may have also been caused by the mechanical excision.

The very high frequency of V1 shoots with aberrant leaves (50% from irradiated main buds) compared with mutation frequencies reported by Lapins (1971) in M1V2* shoots of Bing (12%) or by Thompson (1979) in V2 shoots of Napoleon (8.8%) indicates that only about 20% of these V1 aberrancies are associated with a mutant axillary bud. This is consistent with observation of Lapins et al. (1969) that only 19.6% of aberrant leaves in V1 shoots of apple and peach were associated with mutations in V2 shoots. Lapins (1983) further explained that the primordia of leaves and those of secondary buds have parallel but, presumably, independent ontogeny and that relatively few of the cells associated with leaf initials become involved with secondary bud formation.

Conclusion

- Preliminary irradiation of buds and forcing them in the glasshouse provides reliable information on appropriate range of dosages for use in a large-scale field experiment,
- Accessory bud forcing is greater in the lower (older) part of vigorous scions.
- As a consequence, the LD50 for accessory buds is also greatly influenced by the vigor or age of buds. For basal buds from vigorous scions, the LD50s were approximately 1.5 kR lower than that of main buds. The doses of 2.5–3.0 kR irradiation in air and 4 kR irradiation in water are appropriate doses for accessory buds on vigorous scions.
- Radiosensitivity of buds is affected by irradiation technique. Fractionation of doses resulted in higher LD50s (by ≥1 kR) than acute doses. The same effect is shown by irradiation of buds in water vs. air.
- Irradiation of accessory buds results in slightly larger mutant sectors than irradiation of main buds evidenced by the occurrence of four (0.74%) total shoot mutants in accessory bud shoots vs. none in main bud shoots, and by the greater number of aberrant leaves on shoots showing such aberrancies, i.e. 4.8 in accessory bud shoots and 3.4 in main bud shoots.

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