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Cross Compatibility in the Genus *Anthurium*[1]

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Abstract. **A total of 1592 cross- and self-pollinations were made among 56 species of *Anthurium* Schott. These pollinations included 20 different selfs, 19 different intraspecific cross-combinations, 315 different intragroup interspecific cross-combinations (including reciprocals), and 29 different intergroup cross-combinations (including reciprocals); 280 fruiting spadices yielded 181 seedling populations which flowered and were evaluated both morphologically and chromosomally. Six morphological groups were constructed using primarily the characters considered as important by Engler (1905). Generally the integrity of these 6 groups was confirmed with the possible exception of Groups V and VI. Groups V and VI were more closely related to each other than to any other group, and the characters used in the division of these 2 groups were not as distinctive as those used to divide the other groups. Crossabilities in *Anthurium* tend to follow morphological similarities in the crosses that were attempted.**

The genus *Anthurium* comprises over 500 species which inhabit central Mexico to central South America and the West Indies. Schott (11) grouped 180 *Anthurium* species into 28 sections. Engler (3, 4, 5, 6) described additional species and divided 486 species into 18 sections. Approximately 100 new species have been described since Engler's monograph (6) was published, but the sectional placement of many of these has remained obscure.

Anthurium andreanum Linden is an important cut flower crop in Hawaii, while *A. scherzerianum* Schott is popular as a potted plant in Europe. Other species of horticultural interest are those with variegated, velvety foliage such as *A. warocqueanum* J. Moore and *A. magnificum* Linden.

Anthurium breeding programs have generally been limited to intraspecific hybridizations within *A. andreanum* (1, 7, 8, 9, 10) and *A. scherzerianum.* Engler (6) compiled 18 interspecific hybrids produced before 1905. The present study was initiated to determine cross compatibilities among species within and between constructed morphological groups which might aid future hybridization programs in the genus *Anthurium.*

Materials and Methods

The 57 *Anthurium* species studied are a part of the University of Hawaii collection. Most of the species were collected in Panama and neighboring countries in 1968, but others were obtained from private and commercial sources.[2] The identification of the specimens was based principally upon the taxonomic treatments by Standley (13) and Engler (6). Voucher specimens were prepared and deposited in the Herbarium of the Botany Department, University of Hawaii.

Since the species identifications and sectional placements were initially unknown, the species were divided into 6 distinct morphological groups on the basis of the important Englerian characters of the number of ovules per locule, color and shape of the berry, shape of the inflorescence, and shape and texture of the leaf (Table 1). After the species were identified, comparison of these Groups were made with Engler's sections. Group I (Fig. 1 & Fig. 2) and II (Fig. 3) were separated on the basis of the number of ovules per locule. Groups III (Fig. 4) and IV (Fig. 5) are Engler's Sections *Pachyneurium* and *Schizoplacium,* respectively. Groups V (Fig. 6 & Fig. 7) and VI (Fig. 8) include the remaining species organized into 2 groups on the basis of leaf texture and berry shape and color.

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The 6 groups can be differentiated by the following key:

Berries 3- or more-seeded, shape usually depressed-globose. **Group I**

Berries 2- or fewer-seeded, shape various.

Leaves lanceolate or oblanceolate.

Plants small; leaves 60 cm or less **Group II**

Plants large, coarse; leaves 70 cm or greater. **Group III**

Leaves cordate, hastate-trilobed, palmately-lobed, or pedately-parted.

Leaves palmately-lobed or pedately-parted. **Group IV**

Leaves cordate or hastate-trilobed.

Leaves usually velvety; berry shape apiculate, obovoid, apex dark purple, base lighter (if not purple, then leaf velvety); spadix attenuate. **Group V**

Leaves leathery; berry shape various, color red or orange, infrequently purple; spadix cylindrical or slightly attenuate. **Group VI**

The chromosome numbers of the species were compiled and included in Table 1 with 4 polyploid series evident: 20-40, 24-30-48-84, 28-56, and 30-60-90-ca. 124 (12). Group I contains the greatest chromosomal diversity including all of the polyploid series except 20-40. Group II generally is based upon 2n=30, but also involves a single species *A. scolopendrinum* with 2n=20 and 40. Groups III, IV, V and VI are a part of the polyploid complex based on 2n=30.

Many crosses were made between groups to insure that a representative sample of each group was crossed with each other group, but no attempt was made to cross each species of a group with every other group. Within each group, all possible cross-pollinations were attempted depending on the availability of receptive spadices and pollen. Four species, *A. bakeri, A. scandens, A. scolopendrinum,* and *A. trinerve,* which are apparently naturally self-pollinating were not used as maternal parents, because they were difficult to emasculate. The date and time of pollination, date of abscission or fruit harvest, and no. of seeds per locule were determined. Fruit set was estimated, since repeated pollinations, which were not always possible or practical, would be necessary for an accurate determination. Seed germination (%) was determined on 25 seeds placed on a filter paper in a petri dish. Eight seedlings per cross were grown and evaluated both morphologically and chromosomally.

Results and Discussion

The study involved 1592 pollinations among 57 species. These pollinations included 20 different selfs, 19 different intraspecific cross-combinations, 315 different intragroup interspecific cross-combinations (including reciprocals), and 29 different intergroup cross-combinations (including reciprocals). Fruits were harvested, and germinating seeds were obtained from several of the intra- (Table 2) and intergroup pollinations (Table 3).

Self pollinations (Table 2) resulted in 17 fruiting spadices and 14 flowering hybrid progenies which represented 66.6% of pollinations, while intraspecific cross-pollinations resulted in 34 fruiting spadices and 30 flowering hybrid progenies or 57.7% of pollinations. Although the no. of pollinations is somewhat small, there were no significant differences in the production of offspring between self- and cross-pollination within a species.

Intragroup interspecific pollinations produced 178 fruiting spadices and 128 flowering hybrids (Table 2). Groups II, III, and V gave higher percentages of fruiting spadices and flowering hybrids than Groups I, IV, and VI. However, the no. of combinations of flowering hybrids in Groups II, III, and IV are small, making comparisons of the percentages with binomial confidence intervals nonstatistical.

The low percentage of hybrids obtained in Group I can be expected due to the range of chromosome numbers found in species of this group which include 2n=24, 28, 30, 48 and 84 (12).

The species in Group V are relatively closely related as indicated by their high degree of cross compatibilities. The per-

Table 1. List and groupings of *Anthurium* species examined with chromosome numbers.

Taxa	Engler's section	Chromosome number 2n
Group I		
A. acutangulum Engl.	*Leptanthurium*	30
A. allenii Standl.	*Urospadix*	30
A. chiriquense Standl.	*Urospadix*	30
A. gladiifolium Schott	*Urospadix*	30
A. gracile (Rudge) Lindl.	*Leptanthurium*	30
A. littorale Engl.	*Urospadix*	28
A. ramonense K. Krause	?	30
A. scandens Engl.	*Tetraspermium*	24, 48, 84
A. scherzerianum Schott	*Porphyrochitonium*	30
A. trianae Engl.	*Urospadix*	28, 29 + 1B
A. trinerve Miq.	*Tetraspermium*	24, 30
A. wendlingerii Barroso	*Episeiostenium*	30
Group II		
A. aureum Engl.	*Urospadix*	30, 31
A. bakeri Hook. f.	*Episeiostenium*	30
A. pittieri Engl.	*Oxycarpium*	30
A. scolopendrinum Kunth	*Leptanthurium*	20, 40
A. turrialbense Engl.	*Urospadix*	30
Group III		
A. ellipticum C. Koch & Bouche	*Pachyneurium*	30
A. hacumense Engl.	*Pachyneurium*	30
A. hookeri Kunth	*Pachyneurium*	30, 60
A. joseanum Engl.	*Pachyneurium*	30
Group IV		
A. aemulum Schott	*Schizoplacium*	30, 60
A. digitatum G. Don	*Schizoplacium*	30
A. pentaphyllum G. Don	*Schizoplacium*	60
Group V		
A. clarinervium Matuda	*Cardiolonchium*	30
A. crystallinum Linden & Andre	*Cardiolonchium*	30 + 1B
A. denudatum Engl.	*Belolonchium*	30
A. forgetii N. E. Brown	*Cardiolonchium*	30
A. grande hort.	*Cardiolonchium*	30
A. grandifolium Kunth	*Pachyneurium*	30
A. magnificum Linden	*Cardiolonchium*	ca. 60
A. regale Linden	*Cardiolonchium*	30 + 1B
A. splendidum hort.	*Cardiolonchium*	30 + 2B
A. subsignatum Schott	*Semaeophyllum*	30
A. velutinum? Engl.	*Cardiolonchium*	30
A. venosum? Griseb.	*Cardiolonchium*	30
A. wallisii? Mast.	*Polyneurium*	30 + 2B
A. walujewii Regel	*Cardiolonchium*	30 + 2B
A. warocqueanum J. Moore	*Cardiolonchium*	30 + 3B
A. wullschlaegelii Engl.	*Cardiolonchium*	30
Group VI		
A. andreanum Linden	*Belolonchium*	30
A. baileyi Standl.	?	60
A. concinnatum Schott	*Belolonchium*	30
A. flavo-viride? Engl.	*Belolonchium*	30
A. hoffmannii Schott	*Calomystrium*	30
A. lindenianum C. Koch & Augustin	*Calomystrium*	30
A. micromystrium Sodiro	*Belolonchium*	30
A. nymphaeifolium C. Koch & Bouche	*Calomystrium*	30
A. pichinchae Engl.	*Calomystrium*	30
A. procerum? Sodiro	*Belolonchium*	30
A. ranchoanum Engl.	*Calomystrium*	30
A. rhodostachyum Sodiro	*Digitinervium*	28, 29, 30, 31
A. roraimense N. E. Brown	*Calomystrium*	30
A. subhastatum Schott	*Xialophyllium*	30
A. supianum Engl.	*Belolonchium*	ca. 90
A. triangulum Engl.	*Xialophyllium*	30

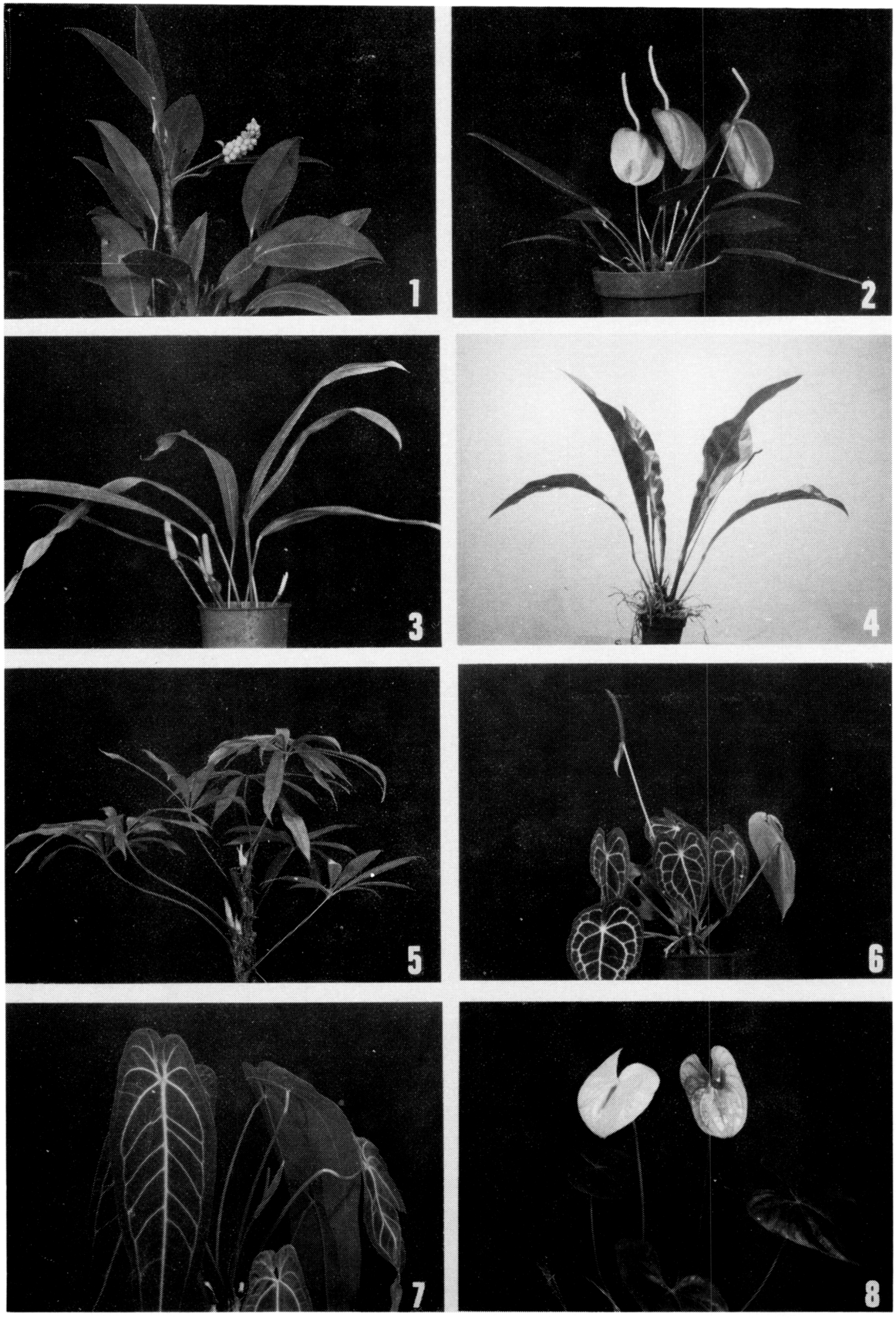

Fig. 1–8. Representative *Anthurium* species of the 6 morphological groups. Fig. 1. *A. trinerve*, Group I, × 1/6. Fig. 2. *A. Scherzerianum,* Group I, × 1/8. Fig. 3. *A. bakeri,* Group II, × 1/8. Fig. 4. *A. ellipticum,* Group III, × 1/20. Fig. 5. *A. aemulum,* Group IV, × 1/12. Fig. 6. *A. clarinervium,* Group V, × 1/12. Fig. 7. *A. warocqueanum,* Group V, × 1/12. Fig. 8. *A. andreanum* 'Uniwai', Group VI, × 1/8.

Table 2. Results of intragroup pollinations in *Anthurium*.

Intragroup pollinations	No. of pollinations	Fruiting spadices harvested No.	Fruiting spadices harvested %	Average % germination	Hybrid progenies flowered No.	Hybrid progenies flowered %
I × I						
Selfs	7	6	86	69.2(6-100)[z]	4	57
Intraspecific[y]	18	8	44	65.3(6-96)	7	39
Interspecific	159	37	23	64.5(0-100)	30	19
Subtotal	184	51	28[x]	65.2(0-100)	41	22[x]
II × II						
Selfs	3	3	100	41.0(0-96)	2	67
Intraspecific	10	9	90	73.1(0-98)	8	80
Interspecific	28	13	46	64.1(0-100)	11	39
Subtotal	41	25	61	64.6(0-100)	21	51
III × III						
Selfs	3	2	67	86.0(72-100)	2	67
Intraspecific	–	–				
Interspecific	26	13	50	32.9(0-100)	8	31
Subtotal	29	15	52	40.0(0-100)	10	34
IV × IV						
Selfs	2	1	50	88.0	1	50
Intraspecific	3	2	67	40.0(0-80)	1	33
Interspecific	22	6	27	21.0(0-78)	3	14
Subtotal	27	9	33	36.7(0-88)	5	19
V × V						
Selfs	3	2	67	74.5(69-80)	2	67
Intraspecific	5	3	60	29.7(0-61)	3	60
Interspecific	131	59	45	48.8(0-100)	38	29
Subtotal	139	64	46	48.7(0-100)	43	31
VI × VI						
Selfs	3	3	100	67.7(43-100)	3	100
Intraspecific	16	12	75	71.3(5-100)	11	69
Interspecific	267	50	19	45.3(0-100)	38	14
Subtotal	286	65	23	51.1(0-100)	52	18
Totals						
Selfs	21	17	81.0[x]		14	66.7[x]
Intraspecific	52	34	65.4		30	57.7
Interspecific	633	178	28.1		128	20.2
Grand total	706	229			172	

[z]The numbers in parenthesis indicate the range of observed values.

[y]Includes intraspecific crosses other than selfs.

[x]These percentages were determined from the totals.

centages of fruiting spadices and flowering hybrids would probably have been higher if not for the common presence of B chromosomes in this group which can affect viability (2, 12).

The lowest percentages of fruits harvested and hybrids flowered were obtained in Group VI, the most morphologically diverse of the groups. However, *A. andreanum, A. concinnatum, A. hoffmannii, A. lindenianum, A. micromystrium, A. nymphaefolium* and *A. pichinchae* successfully produced hybrids when intercrossed. The close relationship of the above species was also observed by Engler (6). Although Engler did not taxonomically circumscribe these species into the same section, the hybrids that he included between Sections *Belolonchium* and *Cardiolonchium* indicated his awareness of their closeness.

Only a single flowering hybrid progeny was obtained from the intergroup cross of VI × IV (*A. triangulum* × *A. digitatum*). This successful cross suggests the possible misplacement of *A. triangulum,* since flowering hybrids were not obtained between this species and others within Group VI. This cross produced a vigorous, sterile hybrid, but the reciprocal resulted in weak seedlings which died early.

Crosses between Groups V and VI resulted in 6 different flowering progenies: *A. grandifolium* × *A. nymphaeifolium, A. grandifolium* × *A. pichinchae, A. grandifolium* × *A. subhastatum, A. lindenianum* × *A. walujewii, A. subsignatum* × *A. lindenianum,* and *A. walujewii* × *A. concinnatum.* Only 3 species in Group V, *A. grandifolium, A. subsignatum* and *A. walujewii,* were involved in the above crosses. These have leathery leaves like the species of Group VI, but the berry color and shape, and inflorescence color and shape are typical of the species in Group V. These 3 species crossed readily with other species within Group V. Engler also recorded a cross of this type, *A. subsignatum* (Group V) × *A. nymphaeifolium* (Group VI).

The 2 horticulturally important species, *A. andreanum* (Group VI) and *A. scherzerianum* (Group I), were subjected to numerous cross pollinations in order to obtain novel and improved types. Fifty-one different interspecific pollinations were attempted between *A. andreanum* 'Uniwai' and all available species except *A. grande, A. littorale, A. roraimense, A. splendidum,* and *A. trianae.* Interspecific hybrids with *A. andreanum* were obtained only within Group VI with the 6 closely related species, *A. concinnatum, A. hoffmannii, A. lindenianum, A. micromystrium, A. nymphaeifolium,* and *A. pichinchae. Anthurium ornatum,* which is very closely allied to *A. nymphaeifolium,* can also be expected to cross with *A. andreanum* as suggested by Engler (6). A hybrid between *A. andreanum* and *A. veitchii* of Group VI was also recorded earlier. Although hybrids between *A. andreanum* and *A. magnificum, A. warocqueanum,* and *A. walujewii* in Group V were recorded earlier, these crosses were not successful in this study.

Thirty-nine different interspecific pollinations were attempted with *A. scherzerianum,* but none resulted in hybrids. Engler (6) recorded a hybrid, *A. scherzerianum* × (*A. andreanum* × *A. nymphaeifolium*). *Anthurium scherzerianum* which often has more than 2 seeds per berry is most closely aligned with some species in Group I and exhibits considerable morphologic and genetic distinctiveness from *A. andreanum* and the related species of Group VI.

Comparison of the percentages of flowering hybrid progenies produced by the total intragroup interspecific pollinations, 20.2% (Table 2), with the intergroup pollinations, 1.0% (Table 3), indicates that the 6 groupings were effective in separating genetically similar species. Using the binomial confidence intervals, this observed difference is significant at the 1% level. Even if the interspecific pollinations of each group are com-

Table 3. Results of intergroup pollinations in *Anthurium*.

Groups crossed	No. of pollinations	Fruiting spadices harvested No.	Fruiting spadices harvested %	Avg % germination	Hybrid progenies flowered No.	Hybrid progenies flowered %
I × II	116	6	5	0.3(0-2)[z]	0	0
× III	20	0	0	–	–	–
× IV	29	0	0	–	–	–
× V	81	1	1	0	0	0
× VI	171	0	0	–	–	–
II × III	4	0	0	–	–	–
× IV	14	2	14	9.0(0-18)	0	0
× V	23	3	13	29.7(0-89)	0	0
× VI	98	8	8	9.9(0-79)	0	0
III × IV	3	0	0	–	–	–
× V	12	1	8	0	0	0
× VI	37	2	5	0	0	0
IV × V	24	1	4	0	0	0
× VI	56	5	9	17.8(0-81)	1	2
V × VI	198	22	11	20.8(0-100)	7	4
Totals	886	51	5.8[y]		9	1.0[y]

[z]The numbers in parenthesis indicate the range of observed values.

[y]These percentages were determined from the totals.

pared individually with the intergroup pollinations, a significant difference at the 5% level is observed in each case. The intragroup pollinations resulted in numerous hybrids, but only 2 intergroup combinations, III × VI and V × VI, resulted in hybrids.

Generally the integrity of the 6 morphologically constructed groups has been confirmed with the possible exception between Groups V and VI. The data support the importance in *Anthurium* of the Englerian characters which were used to establish these groups. Engler's basic understanding of the natural groupings within *Anthurium* has been confirmed. Nevertheless comparison of the species within Groups I and II with their sectional placement indicates that some species have been misplaced as to section, but this can easily be explained. Engler evidently placed the species into sections without observing the no. of seeds per berry. The apparent exception to the integrity of the morphological groups between Group V and Group VI is not really critical. According to the presented key, these 2 groups are more similar to each other than to any other group. Perhaps this indicates that the characters used in this final division of these 2 groups are not as distinctive as those used to divide the other groups. At least in *Anthurium,* crossabilities tend to follow morphological similarities in the crosses that were attempted.

The data suggest that the species within each group are more closely related to each other than to species of other groups. These groupings of the species can therefore be useful for breeding purposes and for evaluating species relationships. These groupings also suggest that some of the sections recognized by Engler need reexamination, especially the species placed in Groups I and II.

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Effect of Daminozide and NAA on Ca Uptake and Accumulation in 'McIntosh' Apple Seedlings[1]

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Abstract. **Leaves from succinic acid-2,2-dimethylhydrazide (daminozide)-treated seedlings of 'McIntosh' apple (*Malus domestica* Borkh) accumulated significantly more ^{45}Ca than those from 1-napthaleneacetic acid (NAA)-treated seedlings. Stem sections from daminozide-treated seedlings accumulated significantly more ^{45}Ca than stems from control seedlings. Total ^{45}Ca content in daminozide-treated seedlings was significantly greater than in either controls or NAA-treated seedlings. The expected reduction in total shoot length by treatment with daminozide, NAA + daminozide and NAA was noted. The increases in ^{45}Ca content in all treatments appear to be due in part to the concentration effect of reduced shoot growth and in part to an effect of daminozide on rate of uptake.**

The importance of Ca nutrition to apple quality is widely accepted and well documented, but little is known about the effect of growth regulators on Ca absorption and accumulation in vegetative tissues of trees. Shear and Faust (10) have reported that movement of Ca within the tree is affected by the concn and availability of the Ca supply. Once Ca is deposited in leaves it is not readily redistributed to other parts of the plant (9). Calcium mobility in tissues has been initiated by subjecting roots to Ca deficiency (3). Transpiration also has been found to affect Ca movement (11). Mobilization of ^{45}Ca has been demonstrated by dehydrating the plant (1), or by treating it with various chemicals (2, 8, 11, 13). The effect of daminozide and NAA on accumulation and mobilization of Ca in apple trees is important, since the use of these chemicals in the commercial orchard operations is becoming widely accepted. The object of this study was to determine the short-term effect of these growth regulators on Ca uptake and accumulation in vegetative tissues of young apple trees.

Materials and Methods

Twenty potted, greenhouse-grown 'McIntosh' apple seedlings were selected for uniformity and placed in darkened cold storage at 0°C from Nov. 11, 1973, to Feb. 18, 1974, to break dormancy. Immediately after removal from cold storage, the

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