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Crossability of Selected Nontuberous *Solanum* Species¹

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Abstract. Reciprocal crosses of 7 selected nontuberous *Solanum* species, each represented by a single genotype, were performed under greenhouse conditions to assess their levels of crossability. The degree of crossability among these species was determined by fruit set, seeds per fruit, seed germination, and degree of F₁ fertility. As a result of crossing these species *inter se*, 3 categories were established: a) species reciprocally crossable and capable of producing fully fertile F₁ plants (*S. gilo* Raddi x *S. integrifolium* Poir.; *S. gilo* x *S. nodiflorum* Jacq.; *S. nodiflorum* x *S. integrifolium*); b) species unilaterally crossable (*S. indicum* L. x *S. incanum* L.; *S. gilo* x *S. incanum*; *S. macrocarpon* L. x 21–73); and c) species reciprocally noncrossable (*S. gilo* x *S. indicum*). Several genotypes of eggplant (*S. melongena* L.) were assessed for their crossability with wild species to investigate the possibility of gene transfer to improve commercial cultivars.

Solanum is a very large and important genus in the Solanaceae, containing about half of the 2200 species in this family (9). Crops of economic importance in this species are potato (*S. tuberosum* L.) and eggplant (*S. melongena* L.). The eggplant is the most horticulturally important representative of the nontuberous group.

In contrast to the tuberous group of *Solanum* species, which has been studied extensively, there has been relatively little research dealing with crossability and hybridization in the nontuberous group (5). The potential value of certain wild *Solanum* species (specifically the resistance to verticillium wilt and cluster-bearing habit) was recognized by Nasrallah and Hopp (6), but these authors reported incompatibility or F₁ pollen sterility for crosses involving eggplant and related *Solanum* species. The crossability and hybridization studies of the other nontuberous species have been generally fragmentary or inconclusive (7, 8) and the results often contradictory (5, 6).

A knowledge of crossability and breeding behavior of selected interspecific *Solanum* crosses may aid the plant breeder in the

improvement of existing eggplant cultivars. Intraspecific variation will continue to be the primary source of genetic variability; however, interspecific hybridization should not be overlooked as a means of enriching the general genetic pool for improving economically important varieties.

Materials and Methods

All seeds were obtained from W. R. Langford, Coordinator, Regional Project S–9, Southern Regional Plant Introduction Station, Experiment, GA 30212. One *Solanum* accession, designated 21–73, has been tentatively identified by one of the authors (Pollack) as an African variety of *S. macrocarpon* L. This accession was included in the present research because it has been shown in previous studies at Rutgers to possess the valuable characteristic of mite resistance. Distinguishing phenotypic characteristics of the parental species are summarized in Table 1.

Seeds were germinated in coarse-grade horticultural vermiculite, and while still in the cotyledon stage, the seedlings were transplanted into 5-cm plastic pots containing a sphagnum peat-moss-vermiculite soilless mix. Three to 4 weeks later, the seedlings were transplanted into 20-cm plastic pots. A pad watering system was used and the plants were fertilized every other week with a 15N–6.4P–12.4K water-soluble fertilizer. Aphids and other greenhouse insects were controlled by periodic applications of a systemic insecticide.

Reciprocal crosses of 7 selected nontuberous *Solanum* species, represented by a single genotype, were performed under controlled greenhouse conditions during the winters of 1977–78 and 1978–79. The species were not used in all combinations of crosses, due to difficulty in synchronizing the flowering of both

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Table 1. Distinguishing phenotypic characteristics of 7 *Solanum* species, each represented by a single genotype.

Accession	Phenotypic characteristics			
	Stem	Leaf	Flower	Fruit
21-73 (An African line acquired by B. L. Pollack)	Green, smooth, spineless.	Smooth, glossy, spineless.	1-2 per cluster, petals light violet.	Round, borne singly, dark green striped immature; yellow when mature.
<i>S. gilo</i> G-2563	Green, hairy, spineless.	Hairy, spineless.	1-4 per cluster, petals white.	Round, usually single, light green striped immature; red when mature.
<i>S. incanum</i> PI 381155	Purple, hairy, small spines.	Hairy, spineless.	1-4 per cluster, petals light violet.	Oval, borne singly, purple immature; brown when mature.
<i>S. indicum</i> PI 194789	Purple, hairy, spineless.	Hairy, spineless.	1-3 per cluster, petals white, each with a central purple stripe.	Round, usually singles, light green immature; red mature.
<i>S. integrifolium</i> PI 374695	Dark purple, hairy, spiny.	Hairy, spiny.	3-12 per cluster, petals white, each with a central purple stripe.	Oblate, some singles but usually in clusters, dark green immature; red mature.
<i>S. macrocarpon</i> PI 370051 (Listed as <i>S. melongena</i> by S.R.P.I.S.)	Purple, smooth, spineless.	Smooth, glossy, spineless.	4-10 per cluster, petals violet.	Round, borne singly, pale white immature; reddish-brown mature, with the peel cracking.
<i>S. nodiflorum</i> PI 247828	Dark purple, smooth, spineless.	Smooth, dull, spineless.	5-14 per cluster, petals white, each with a central purple stripe.	Round to oblate, some singles but usually in clusters, dark green immature; red mature.

parents. The low number of pollinations performed in certain crosses was also a consequence of this difficulty.

The degree of crossability among the species was determined by fruit set, number of seeds per fruit, seed germination, and degree of F₁ fertility from successful intercrosses of the species. Fertility was evaluated subjectively using an arbitrary scale where a plant with no fruit was assigned a value of 1, while a plant judged to have full fruit set was assigned a value of 9. Plants with intermediate fruit set received ratings between 1 and 9.

Results

To assess the degree of crossability between any 2 species, it was necessary to determine the reproductive capacities of the parental lines (Table 2). The range of seeds per fruit was from

194 in *S. integrifolium* to 957 in *S. incanum*. Germination ranged from 20% in *S. nodiflorum* to 94% in *S. macrocarpon*. The extremely low percentage of germination of *S. nodiflorum* seeds is not considered to be an accurate estimate for this species, however, because only 1 fruit was sampled, and it is suspected that this fruit was not fully mature when harvested. In 6 of the 7 genotypes, all seedlings transplanted reached maturity and were highly fertile. The vigor of the *S. nodiflorum* seedlings that did germinate was so poor that none were transplanted.

Crossability data for reciprocally crossable *Solanum* species and survival rates of their hybrid progenies are presented in Table 3. Fruit set ranged from 1 in the crosses *S. gilo* × *S. integrifolium*, *S. nodiflorum* × *S. integrifolium*, *S. gilo* × *S. nodiflorum*, and *S. nodiflorum* × *S. gilo* to 4 in the cross *S. integrifolium* × *S. gilo*.

Table 2. Comparison of 6 reproduction parameters from 7 parental genotypes of *Solanum* species.

Species	No. fruits sampled	No. seeds/fruit	Seed germination (%)	No. seedlings transplanted	No. seedlings matured	Fertility ^z
21-73	4	912	92	6	6	9
<i>S. gilo</i>	2	532	50	6	6	9
<i>S. incanum</i>	1	957	85	6	6	9
<i>S. indicum</i>	10	461	71	6	6	9
<i>S. integrifolium</i>	10	194	75	6	6	9
<i>S. macrocarpon</i>	5	825	94	6	6	9
<i>S. nodiflorum</i>	1	201	20	0	---	---

^zFertility scale: 1 = no fruit set; 9 = full fruit set.

Table 3. Reciprocal crossability of *S. integrifolium*, *S. gilo*, and *S. nodiflorum* and survival rate of their hybrid progenies.

Cross	No. flowers pollinated	No. fruit set	No. seeds/fruit	Percent of female O.P.	Seed germination (%)	No. seedlings transplanted	No. seedlings flowered	Fertility ²
<i>S. integrifolium</i> × <i>S. gilo</i>	10	4	144	74.2	100	18	18	9
<i>S. gilo</i> × <i>S. integrifolium</i>	10	1 ^y	---	---	---	---	---	---
<i>S. nodiflorum</i> × <i>S. integrifolium</i>	10	1	13	6.5	100	18	18	9
<i>S. integrifolium</i> × <i>S. nodiflorum</i>	10	3	13	6.9	100	18	18	9
<i>S. gilo</i> × <i>S. nodiflorum</i>	10	1 ^y	---	---	---	---	---	---

²Arbitrary fertility scale, where 1 = no fruit set and 9 = full fruit set.

^yFruit obtained as a result of earlier pollinations. No further data recorded.

Numbers of seeds per fruit for the crosses were lower than numbers of seeds per fruit counted in open-pollinated fruits of the female parents (Table 2). Numbers of seeds per fruit for the cross *S. nodiflorum* × *S. integrifolium* and its reciprocal were very low, representing only 6.5% and 6.9%, respectively, of the numbers of seeds found in open-pollinated fruits of the female parents. Number of seeds per fruit for the cross *S. integrifolium* × *S. gilo* was considerably higher, representing 74.2% of the number of seeds counted in an open-pollinated fruit of *S. integrifolium*. As indicated, seeds were not counted in fruits of the crosses *S. gilo* × *S. integrifolium*, *S. gilo* × *S. nodiflorum*, and *S. nodiflorum* × *S. gilo*. These fruits were obtained as a result of earlier pollinations, and although further data were not determined, seeds from these fruits were germinable and produced a small number of F₁ plants. Seed germination was 100% for the crosses *S. integrifolium* × *S. gilo*, *S. nodiflorum* × *S. integrifolium*, and *S. integrifolium* × *S. nodiflorum*. For these 3 crosses, all the transplanted seedlings flowered and were highly fertile.

Crossability data for unilaterally crossable *Solanum* species and survival rates of their hybrid progenies are presented in Table 4. Fruit set ranged from 1 in the cross *S. indicum* × *S. incanum* to 5 in the cross *S. gilo* × *S. incanum*. Again, numbers of seeds per fruit for the crosses were found to be less than numbers of seeds per fruit in open-pollinated fruits of the female parents (Table 2). The crosses *S. gilo* × *S. incanum* and *S. macrocarpon* × 21-73 bore fruits containing only 14.1 and 8.7%, respectively, of the number of seeds found in open pollinated fruits of their respective female parents, while this figure was much higher (85.5%) for the crosses *S. indicum* × *S. incanum*. Percentage of germination was quite high for all 3 crosses, and all seedlings transplanted were vigorous and flowered profusely. However, fruit set was very low for the F₁ hybrid *S. indicum* × *S. incanum*, and the hybrid *S. gilo* × *S. incanum* set no fruit at all. In contrast, the F₁ hybrid *S. macrocarpon* × 21-73 exhibited full fruit set.

The only species determined to be reciprocally noncrossable were *S. gilo* and *S. indicum*. In attempted pollinations in both directions, none were successful. It should be pointed out that data on combinations of species other than those described above

are incomplete. For example, our data indicate that *S. indicum* is crossable with both *S. nodiflorum* and *S. integrifolium* when *S. indicum* is used as the male parent, but we do not know the crossability relationships among these species when *S. indicum* is the female parent. Similarly, 5 attempts to obtain hybrids involving other species were unsuccessful in one direction (*S. macrocarpon* with *S. gilo*, *S. incanum*, *S. indicum*, and 21-73 with *S. nodiflorum*, *S. indicum*). Reciprocal pollinations were not performed due to problems in flowering synchronization.

F₁ interspecific hybrids of the reciprocally crossable species were subsequently evaluated for number of seeds per fruit and percentage of seed germination (Table 5). The F₂ populations resulting from these seeds were grown under field conditions, and their fertility was judged as before, on a scale of 1 to 9. In the F₁ generations, an even further reduction in the number of seeds per fruit was observed. Extreme examples were the F₁ of *S. integrifolium* × *S. nodiflorum* and its reciprocal. Averages of only 0.5 and 0.1 seeds/fruit were determined, respectively, from 323 and 292 fruits of these 2 hybrids. Fruits from the F₁ hybrid *S. integrifolium* × *S. gilo* contained an average of 12.4 seeds, but even this represents only 6.4% of the number of seeds in a typical fruit of the female parent.

Germination of F₂ seed was quite high, ranging from 87 to 95%. All transplanted seedlings flowered, and the fertility of the populations ranged from 8.0 for the cross *S. gilo* × *S. integrifolium* to 8.9 for the cross *S. integrifolium* × *S. nodiflorum*.

As a result of the crossing behavior of the selected *Solanum* species, a polygon was prepared to summarize the findings (Fig. 1). Reciprocal crosses were attempted whenever possible, but problems in synchronizing the flowering of both parents sometimes prevented this. It should be emphasized that the crossability relationships suggested in Fig. 1 were based on small numbers of pollinations and more detailed studies are desirable for confirmation. Six levels of crossability were detected, ranging from complete failure of the cross to success in obtaining not only the F₁, but also fertile F₂ generations. The polygon illustrates the 3 crossability patterns: 1) species reciprocally crossable; 2) species unilaterally crossable; and 3) species reciprocally noncrossable. The cross *S. gilo* × *S. integrifolium*

Table 4. Unilateral crossability of 4 *Solanum* species and survival rate of 3 hybrid progenies.

Cross	No. flowers pollinated	No. fruit set	No. seeds/fruit	Percent of female O.P.	Seed germination (%)	No. seedlings transplanted	No. seedlings flowered	Fertility ²
<i>S. indicum</i> × <i>S. incanum</i>	5	1	394	85.5	99	18	18	2
<i>S. gilo</i> × <i>S. incanum</i>	5	5	75	14.4	95	18	18	1
<i>S. macrocarpon</i> × 21-73	10	3	72	8.7	94	18	18	9

²Arbitrary fertility scale, where 1 = no fruit set and 9 = full fruit set.

Table 5. Seed set, germinability, and fertility in the selected F₁ interspecific *Solanum* hybrids and resultant F₂ populations.

Cross	F ₁ hybrids			F ₂ derivatives			
	No. fruits sampled	No. seeds/fruit	Percent of female O.P.	Seed germination (%)	No. seedlings transplanted	No. seedlings flowered	Fertility ^z
<i>S. gilo</i> × <i>S. integrifolium</i>	34	7.9	1.5	87	42	42	8.0
<i>S. integrifolium</i> × <i>S. gilo</i>	40	12.4	6.4	95	65	65	8.7
<i>S. integrifolium</i> × <i>S. nodiflorum</i>	323	0.5	0.3	93	30	30	8.9
<i>S. nodiflorum</i> × <i>S. integrifolium</i>	292	0.1	0.1	94	10	10	8.1

^zArbitrary fertility scale, where 1 = no fruit set and 9 = full fruit set. Numbers represent population means.

could be effected in either direction, as indicated by the heavy black arrows. The same results were obtained for the cross *S. integrifolium* × *S. nodiflorum*. The combination *S. gilo* × *S. nodiflorum* was successful in both directions, however, F₂ seedlings lacked vigor and did not flower. The unilaterally crossable combinations of species, *S. indicum* × *S. incanum*, *S. gilo* × *S. incanum*, *S. macrocarpon* × 21-73, are illustrated by a dotted line in the direction of cross failure, and a line in the opposite direction indicating the level of crossability. The only species determined to be reciprocally noncrossable, *S. gilo* and *S. indicum*, are illustrated by dotted lines in both directions.

In addition to the main crossability study, several genotypes of *S. melongena* were assessed for their crossability with some of the wild species. Since these species have certain desirable horticultural characteristics, there is the possibility of improving commercial eggplant varieties by transfer of particularly desirable genes. Results of this additional study are summarized in Fig. 2. Cluster-bearing habit and mite resistance are desirable characters that may be transferred in the future to commercial cultivars. Although F₁ and BC₁ characters were not evaluated,

we were successful in crossing certain plant introductions of *S. melongena* with *S. integrifolium*, *S. macrocarpon*, and *S. nodiflorum*. It can be seen from Fig. 2 that *S. macrocarpon* PI 370051, when used as male parent, was crossable with *S. melongena* PI 386251, and when used as female parent, was crossable with *S. melongena* PI 198330, 321018, and 381287.

Discussion

In terms of crossability, our data indicate that *S. gilo* and *S. integrifolium* are very closely related, as are *S. integrifolium* and *S. nodiflorum*. *S. gilo* and *S. nodiflorum* are somewhat less closely related, as are *S. macrocarpon* and 21-73.

S. indicum, when used as the male parent, was crossable with both *S. integrifolium* and *S. nodiflorum*, although it was not crossable in either direction with *S. gilo*. This finding is in conflict with results obtained by Nasallah and Hopp (6), who obtained fertile F₁ plants from the cross *S. gilo* × *S. indicum* and its reciprocal. Narasimha Rao (5) reported that the cross *S.*

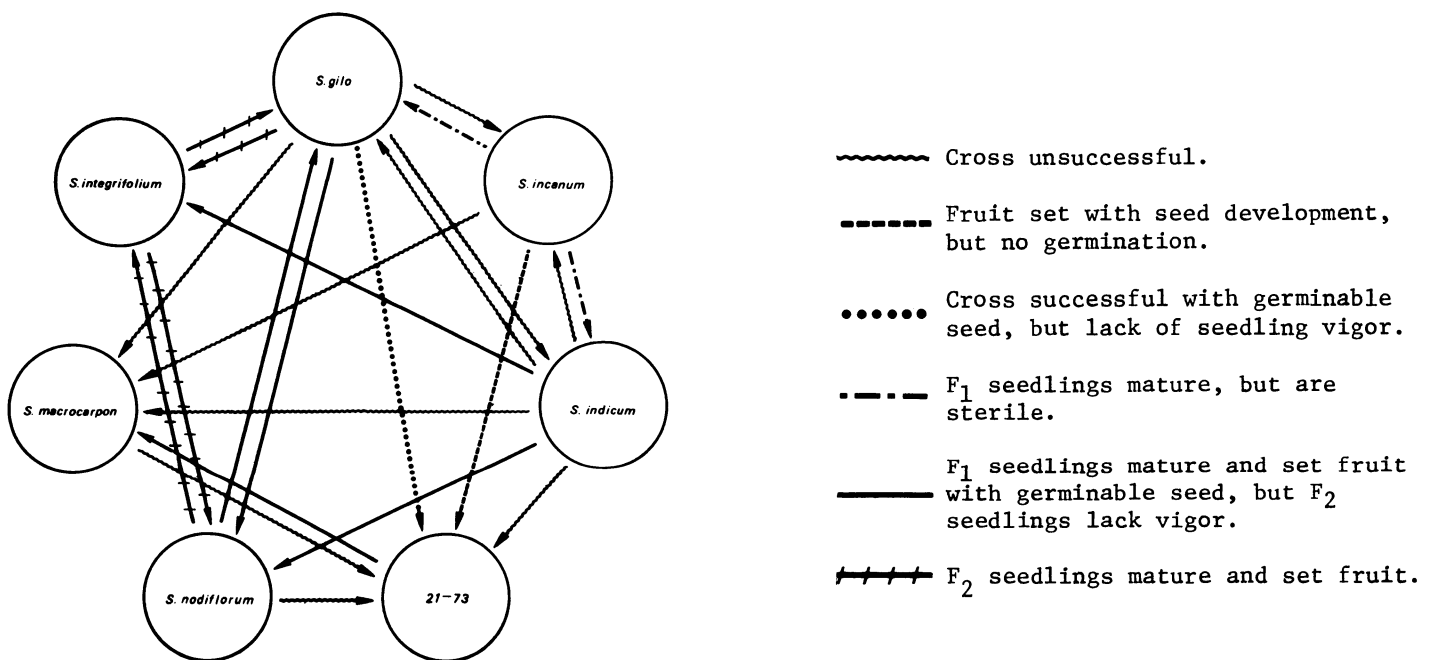


Fig. 1. Crossability polygon among 7 selected species of *Solanum*. Arrowheads point toward female parents. An absence of lines between any 2 species indicates that no pollinations were performed due to problems in flowering synchronization.

<i>Solanum</i> spp. <i>S. melongena</i> ♀ × ♂	<i>gilo</i> G-2563	<i>integrifolium</i> Pl. 374695	<i>macrocarpon</i> Pl. 370051	<i>nodiflorum</i> Pl. 247828
Pl. 115507	Z	Z	A	B
Pl. 115509	A	Z	Z	Z
Pl. 164751	Z	Z	B	Z
Pl. 198332	Z	C	Z	C
Pl. 386251	Z	C	C	Z

<i>S. melongena</i> ♀ × ♂ <i>S. macrocarpon</i>	Pl. 115507	Pl. 198330	Pl. 321018	Pl. 370046	Pl. 381287
Pl. 370051	A	C	C	A	C

Fig. 2. Crossability chart for various genotypes of *S. melongena* and 4 other *Solanum* spp.

- A = Fruit set with seed development, but no germination.
 B = F₁ very unfruitful; fruit that set contain germinable seed.
 C = F₁ uniformly fruitful, with germinable seed.
 Z = No pollinations performed due to problems in flowering synchronization.

indicum × *S. gilo* was successful, while the reciprocal failed. It is possible that the use of different parental genotypes or variations in environmental conditions were responsible for inconsistent results. Other factors that can cause variability include pollination technique and relatively small number of pollinations.

While many attempts at interspecific hybridization have been reported previously for *S. gilo*, *S. integrifolium*, *S. indicum*, *S. incanum*, and *S. macrocarpon* (5, 6, 10, 11, 12, 13), there is a general lack of information about the relationships of *S. nodiflorum*. Omidiji (7) reported that this species was reciprocally crossable with *S. nigrum* and he obtained F₁ hybrids, but the "nodiflorum" genotype ('Odu') was later reidentified as a variety of *S. nigrum* (8). This particular variety was phenotypically very similar to *S. nigrum* var. *Ogumo* and was also reported to be hexaploid.

The species exhibiting unilateral crossability are of special genetic interest. In crossing related species, it has been found frequently that the hybrid can be obtained in one direction only. This phenomenon, termed "unilateral interspecific incompatibility," has been reported in the Solanaceae and Scrophulariaceae by Lewis and Crowe (4), who found that pollen tube growth is inhibited in the cross self-incompatible (SI) style × self-compatible (SC) pollen.

It is generally agreed that self-incompatibility in the angiosperms is primitive and self-compatibility a derived condition. But how has the evolution of SC species occurred? It is known that the pollen of certain SC species (*Lycium chinense* and *Antirrhinum majus*) is not inhibited in styles of related SI species (1, 4). It is proposed that these examples represent cases of species that have been SI in the past and have recently changed to SC.

Although all the species in this research are SC, the phenomenon of unilateral interspecific incompatibility was observed in several combinations. Perhaps certain of the unilaterally crossable species in this study, like *L. chinense* and *A. majus*, were SI in the past and have recently changed to SC. *S. nodiflorum*, *S. incanum*, and 21-73 are examples whose crossability behavior could be explained along these lines. If they are recent SC species, their styles could be expected to inhibit the pollen of other SC species, such as *S. gilo*, *S. indicum*, and *S. macrocarpon*. Self-incompatibility has been reported in many of the diploid tuberous *Solanum* species (2) and in certain wild species of the related genus *Lycopersicon* (3).

From a practical point of view, those combinations of species that are reciprocally crossable are most interesting. The production of fertile F₁ plants from these combinations indicates that recombination between the genomes of the species and production of new combinations of genetic material are possible. Also of particular practical interest are the successful crosses of several *S. melongena* genotypes with *S. integrifolium*, *S. nodiflorum*, and *S. macrocarpon*. Both *S. integrifolium* and *S. nodiflorum* exhibit cluster-bearing habit, a character useful in breeding for increased yield, and an accession of *S. macrocarpon* has shown promise for incorporating mite resistance into commercial eggplant cultivars (13). It should be pointed out that crosses involving *S. integrifolium* and *S. nodiflorum* were possible only when *S. melongena* was used as the female parent, while crosses involving *S. macrocarpon* were possible also when *S. melongena* was used as the male parent.

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Prestorage and Poststorage Starch Levels in Chemically and Hand-defoliated 'Delicious' Apple Nursery Stock¹

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Abstract. To investigate the effects of chemical and hand-defoliation on starch levels in apple nursery stock, 1-year-old commercially graded whips of 'Delicious' apple (*Malus domestica* Borkh.) were planted in April 1977 and 1978, headed at 30 cm, and later trained to a single vigorous shoot. Plots were hand-defoliated on October 1, 15, or 30. Additional plots were treated with 1, 2, or 3 applications at 5-day intervals, starting October 5, of 1.5% Dupont WK surfactant (principle functioning agent, trimethylnonylpolyethoxyethanol) alone or plus 20 ppm (2-chloroethyl) phosphonic acid (ethephon). All trees were dug Nov. 15 in both years. Starch levels increased as hand-defoliation was delayed and usually decreased with multiple as compared to single chemical applications. These effects were evident both prestorage and poststorage, with starch levels decreasing during storage in roots and stems but changing little in buds. The amount of shoot growth produced on the trees during the summer following storage and replanting displayed a pattern somewhat like that of the levels of starch in the trees. Delaying hand-defoliation until October 30 produced the highest starch levels (hand- or chemically treated) both years at April planting time.

Because deciduous tree fruit nursery stock is usually heavily fertilized and irrigated, natural defoliation is often late, causing concern when cold weather approaches. Since nurserymen may not wish to risk tree losses from cold damage by waiting for natural leaf fall and since trees do not store well with leaves attached, considerable effort has been directed toward finding chemical treatments to speed defoliation and replace the usual practice of hand-stripping of leaves.

Dupont WK surfactant (DWK) alone or in combination with ethephon is commercially important for apple nursery-stock defoliation (5). However, poststorage condition and postplanting performance of commercially treated stock is sometimes substandard. Since starch is the main storage carbohydrate in apple (1, 4, 6, 9), reduced levels in treated stock could result in reduced storability and poor postplant performance. To help explain the occasional substandard performance of treated stock, pre- and poststorage levels of starch in 'Delicious' apple nursery stock were measured and compared to levels in untreated stock and in stock that had been hand-defoliated.

Materials and Methods

One-year-old commercially graded whips of 'Delicious' apple nursery stock were planted in 1 × 3m rows in April 1977 and 1978 at the Washington State University experimental farm in Pullman. Trees were headed back to 30 cm from the ground after planting and later trained to 1 vigorous shoot. The trees were fertilized and irrigated uniformly to produce vigorous growth throughout the summer.

Plots were hand-defoliated on Oct. 1, 15, or 30 during both years. Chemical treatments were applied on Oct. 5, Oct. 5 and 10, or Oct. 5, 10, and 15. The chemicals used were 1.5% DWK alone or in combination with 200 ppm ethephon, typical commercial treatments. Plots consisted of 9 trees each and were replicated 4 times. Chemicals were applied to runoff with a hand-sprayer. Control trees were not treated. The degree of defoliation was visually estimated (Table 1) and trees were dug on Nov. 15 each year. Six trees from each plot were stored at 3°C with roots in moist sawdust. Three trees from each plot were washed, placed in plastic bags, and frozen at –20° for later analysis. In April, half of the trees that had been stored at 3° was washed and frozen at –20° for analysis while the other half was planted for observation and measurement of shoot growth.

Frozen trees were divided into buds, stems, and roots and then weighed. Tissue samples were lyophilized, ground, and stored in air-tight vials in a desiccator with anhydrous CaSO₄. A weighed quantity of tissue was extracted with 80% ethanol. The ethanolic extract residue was dried in a vacuum oven at 60°C, weighed, and kept in air-tight vials in a desiccator for later starch analysis.

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