

Antixenotic and Antibiotic Resistance in *Apium* Species to *Liriomyza trifolii* (Diptera: Agromyzidae)

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ABSTRACT The potential for resistance to the leafminer *Liriomyza trifolii* (Burgess) in *Apium* L. species was evaluated in field trials and no-choice tests in the laboratory. In field trials with 159 accessions from throughout the world, only *A. leptophyllum* (Pers.) F. Muell. from Australia (A162), *A. prostratum* ssp. *prostratum* var. *filiforme* (A. Rich.) Kirk. from Australia (A230), and Chinese smallage 'Huang Hsin Late' from Taiwan (A16), consistently and significantly exhibited resistance as measured by an index of infestation (percentage of leaves mined per plant). Only *A. leptophyllum* completely lacked mining, probably due to resistance based on a filiform leaf architecture. No-choice experiments evaluating leafminer oviposition and development on promising accessions demonstrated that some accessions could reduce leafminer population growth. In these tests, only *A. prostratum* (A230) was not fed or oviposited upon. Although the other accessions produced no differences in developmental time from egg to pupa, numbers of mines per plant, or the ratio of mines to punctures, significant differences in numbers of pupae and adults, and the ratios of pupae to mines and adults to pupae, indicated substantial antibiosis. Incorporation of these accessions into a celery breeding program and programs for integrated and pesticide resistance management are discussed.

KEY WORDS Insecta, resistance, antibiosis, antixenosis

THE LEAFMINER *Liriomyza trifolii* (Burgess) has caused substantial economic losses in the major vegetable production areas of the United States (Leibee 1984, California Celery Research Advisory Board 1985). These losses have been stimulated by the rapid development of insecticide resistance or tolerance by the leafminer (Parrella 1987). Unfortunately, development of pesticide resistance often leads to the use of maximum rates and minimum intervals of pesticide application, which further exacerbates the problem. As a result, many of the pesticides available for use against leafminers and other key pests in vegetables now selectively remove the key parasites associated with *Liriomyza* species, causing rapid and unchecked growth in leafminer populations (Oatman & Kennedy 1976, Johnson et al. 1980, Trumble & Toscano 1983).

Resistance development and parasite mortality, when coupled with an increasing concern for the environment and the related decrease in availability of pesticides following new legislation addressing the topics of human toxicity and groundwater contamination, clearly demonstrate a need for the development of less pesticide-intensive systems. Ideally, new management systems for *L. trifolii* will maximize leafminer suppression and minimize both the potential for development of pesticide resistance and any negative impact on leafminer parasites (Trumble 1985). One approach

to this problem is to exploit alternative control techniques such as host plant resistance (Kennedy et al. 1987). Therefore, the primary goals of our research were to assess a diverse selection of *Apium* L. accessions for potential resistance in the field, then to evaluate the most promising accessions in the laboratory for possible impact on leafminer population development.

Materials and Methods

Field Experiments. A field trial including 156 accessions of celery and related plants was arranged in three replicates of 10 plants each in a randomized complete block design. The planting was established at the University of California's South Coast Field Station in Santa Ana, Calif., during the summer of 1985. Plants were transplanted with 18-cm spacings on drip-irrigated, single-row beds 1 m apart. Fertilizer and irrigation schedules were consistent with local commercial celery production practices. One application of methomyl at 0.4 kg (AI)/ha was made during mid-August to limit damage by *Spodoptera exigua* (Hübner) and *Trichoplusia ni* (Hübner). This treatment also maximized the population pressure of *L. trifolii* through the selective removal of associated parasites (Trumble & Toscano 1983).

L. trifolii mining in the foliage of all plants was monitored every 2 wk for 2 mo using an infestation index where the values 0, 1, 2, 3, and 4 equal 0, 1-25, 26-50, 51-75, and >75% of the leaves per

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plant with at least one live larva present, respectively. No effort was made to quantify the age of larvae that did not complete development. Data were analyzed following an arcsine transformation by analysis of variance (ANOVA) and the Student-Newman-Keuls test (SAS Institute 1985, $P < 0.01$).

Laboratory Experiments. To determine if selected accessions with minimal leafminer damage in the field tests were actually unsuitable for *L. trifolii* larval development or simply less preferred for oviposition, no-choice challenges were designed for some of the most promising accessions and three susceptible controls, 'Tall Utah' 5270 HK (*A. graveolens* L.), 'Lepage race Istra' (A209), and *A. prostratum* Vent. (A161) from South Africa. Also included were accessions of two wild species, *A. chilense* Hook and Arn. (A73) from Chile and *A. panul* Reiche (A160) from Chile, which appeared promising in preliminary laboratory experiments, as well as F_1 hybrids obtained between *A. chilense* or *A. panul* and cultivated celery, 'Tall Utah' 5270 HK (A41). The F_1 's, confirmed as hybrids by isozyme electrophoresis (Ochoa & Quiros 1986), were morphologically intermediate to the parental species.

The plant materials used in the experiment were standardized to the extent possible. All plants were germinated concurrently and exposed to the same nutrient, moisture, and light regimes in a greenhouse. Leaf area on the test plants was standardized to 200–300 cm² per plant (Li-Cor 3000 Portable Leaf Area Meter, Li-Cor Inc., Lincoln, Nebr.) by removing the youngest leaves and any visibly senescent foliage. This left the largest (25–30 cm) and most attractive petioles for oviposition and larval development (Tryon & Poe 1979). Although this minor trimming of the plants potentially could induce production of defensive chemicals, structural damage caused during transplanting (i.e., stripping of excess petioles or mowing of the top 6–8 cm of foliage), by feeding of leafminers or lepidopterous larvae, or by common cultural practices such as side dressing of fertilizer, also would stimulate induced responses. Thus, the advantages associated with standardizing plant size were considered to outweigh the possible interference of induced responses.

Adult *L. trifolii* used in these trials were obtained from a celery field in Orange County, Calif., and maintained in a laboratory colony reared on 'Tall Utah' 5270 HK celery. Although Tavormina (1982) and Via (1984a,b) demonstrated that closely related species of *Liriomyza* developed a preference for the host species from which they had been reared, Via found no differences in average responses (pupal weight, developmental time) to different host species. Thus, 'Tall Utah' was chosen for laboratory maintenance because this is the most common *Apium* species planted in California, and *L. trifolii* will be forced to make a similar transition to alternate hosts under field conditions if new accessions become widely used. All *L. trifolii* adults

used in this study were 3 d old and had been fed only a 20% honey solution prior to exposure to the test plants.

Plants were placed individually in 11.4-liter cylindrical containers and exposed to five pairs of adult *L. trifolii* for 2 h. Ten replicates were evaluated, each consisting of one plant from each of 11 accessions. Plants were held in an environmental chamber set for a photoperiod of 16:8 (L:D) and $26.7 \pm 1^\circ\text{C}$. After 3 d, the feeding-oviposition punctures were counted. The numbers of mines per plant were assessed after 4–5 d. Plants then were tilted on their sides so that larvae emerging from the leaves would drop into a tray filled with sand. Numbers of larvae and pupae were recorded daily until no live larvae remained in the foliage. Pupae from each plant were held in the environmental chamber for at least 2 wk, at which time the numbers of males and females successfully reaching the adult stage were recorded. Developmental data were analyzed with ANOVA and the Student-Newman-Keuls test (SAS Institute 1985, $P < 0.01$); ratios of feeding punctures/mines, pupae/mines, adults/pupae, and females/males were analyzed similarly following an arcsine transformation.

Results and Discussion

Field Experiments. All accessions, except for the wild species *A. leptophyllum* (Pers.) F. Muell. from Australia (A162), were mined by *L. trifolii*. However, the variation in susceptibility-attractiveness was greatest among accessions during peak population pressure of the leafminer in late August (Table 1). Although significant ($F = 2.68$; $df = 155, 312$; $P < 0.001$) variation occurred in the number of mines per plant during this period, only Chinese smallage 'Huang Hsin Late' (A16) from Taiwan, and the wild species *A. prostratum* (A230) ssp. *prostratum* var. *filiforme* (A. Rich.) Kirk. from Australia, consistently had fewer mines on subsequent sampling dates.

The lack of leafminer damage in *A. leptophyllum* might be related to its filiform leaf structure which may not sustain feeding or oviposition due to a narrow architecture. Thus, there is no guarantee that this antibiosis-based resistance (terminology after Renwick [1983]) would be maintained when the filiform leaf type is altered. In addition, this species has a genomic number of $x = 7$, which is quite distant taxonomically from commercial celery (genomic number, $x = 11$). Because this species does not hybridize sexually (Ochoa & Quiros 1986), its immediate use in a celery breeding program would be precluded. Therefore, *A. leptophyllum* was not included in subsequent laboratory experiments.

The variability in mining observed between accessions in these field trials may not be particularly important in a large acreage commercial planting. *L. trifolii* may feed and develop large

Table 1. Resistance in *Apium* accessions to *L. trifolii* in field trials

Description	Accession #	USDA PI # ^a	Leaf-mining index ^b
Celeriac, Turkey	A1	PI175591	3.33abc
Celeriac, Turkey	A2	PI176870	4.00a
Smallage, Ethiopia	A3	PI196831	3.00bc
Smallage, Iran	A4	PI222702	3.33abc
Celery, Iran	A5	PI222967	3.67ab
Celeriac, Iran	A6	PI223333	3.33abc
Smallage, Iran	A7	PI226624	3.67ab
Smallage, Iran	A8	PI229526	3.67ab
Celery, 'South Australian White'	A9	PI234596	3.33abc
Celery, 'Giant Green Dewcrisp'	A10	PI234597	3.00bc
Celery, Spain	A11	PI257279	3.33abc
Celery, 'Jablkowy'	A12	PI285546	3.00bc
Smallage, 'Hainan'	A15	PI320994	3.33abc
Smallage, 'Huang Hsin Late'	A16	PI320995	2.67cd
Smallage, 'Huang Hsin Medium Late'	A17	PI320996	3.00bc
Celeriac, Turkey	A18	PI344267	3.33abc
Celery, 'Mesten'	A19	PI357325	3.33abc
Smallage, 'Stevi Nikolski'	A20	PI357326	3.67ab
Celeriac, 'Domaser'	A21	PI357327	3.67ab
Smallage, 'Korenest'	A22	PI357328	4.00a
Celeriac, 'Prilepski'	A23	PI357329	3.67ab
Celery, Winter, var. China (0-02)	A24	—	3.33abc
Celeriac, 'Lister'	A25	PI357331	3.67ab
Celeriac, 'Lokalen'	A26	PI357332	3.00bc
Celeriac, 'Kocanski'	A27	PI357333	3.33abc
Smallage, 'Debarski'	A28	PI357335	3.67ab
Celeriac, 'Bitolski'	A29	PI357336	4.00a
Smallage, 'Injilanski'	A30	PI379083	4.00a
Celery, 'Nereski'	A32	PI379085	4.00a
Smallage, Shih Kan lu Chin	A34	PI391543	3.33abc
Celery, 'Transgreen'	A35	—	3.33abc
Celery, 'Tendercrisp'	A36	—	3.33abc
Celery, 'Super Pak'	A37	—	3.67ab
Celery, 'Florida 214'	A38	—	3.33abc
Celery, 'Florida 683 K'	A39	—	3.33abc
Celery, 'Tall Utah' 5270 R	A40	—	3.67ab
Celery, 'Tall Utah' 5270 HK	A41	—	3.67ab
Celery, 'Florimart 19'	A43	—	3.00bc
Celery, 'Summer var.'	A44	—	3.00bc
Celery, '370 Tall Green Light'	A45	—	3.33abc
Celery, 'Asmer Multipak'	A48	—	3.33abc
Celery, 'Clused Lathom Self Blanching'	A49	—	3.00bc
Celery, 'Asmer Jagen'	A50	—	3.67ab
Smallage, San Luis Obispo, CA	A63	—	4.00a
Smallage, Coon Creek, CA	A64	—	3.33abc
Smallage, Canada Honda, CA	A65	—	3.33abc
Smallage, San Luis Obispo, CA	A66	—	3.33abc
Smallage, Casmalia, CA	A67	—	3.67ab
Smallage, China	A68	—	4.00a
Smallage, Oso, Flaco, CA	A69	—	4.00a
Smallage, 'Amsterdam Feiner'	A70	—	4.00a
Celery, 'Deacon'	A76	—	3.67ab
Celery, 'Bishop'	A77	—	3.00bc
Smallage, Inner Mongolia, China	A78	—	3.67ab
Celeriac, 'Gribovski'	A89	—	3.33abc
Celeriac, 'Jablovsky'	A90	—	3.67ab
Celery, 'Golden Spartan'	A91	—	3.33abc
Celery, 'Tall Golden Self Blanching'	A93	—	3.33abc

Table 1. Continued

Description	Accession #	USDA PI # ^a	Leaf-mining index ^b
Celeriac, 'Pragen Reisen'	A94	—	4.00a
Celery, 'Vert De Villeneuve'	A95	—	3.33abc
Celery, 'Blanchato Golden Self Blanching'	A96	—	3.33abc
Celery, 'Vert D. Elne'	A97	—	3.67ab
Celery, 'Giant Pascal'	A98	—	3.00bc
Celery, 'Loret Lathom Self Blanching'	A99	—	3.33abc
Celery, 'Asmer Lathom Self Blanching'	A100	—	3.33abc
Celeriac, Turkey	A101	PI120875	3.00bc
Smallage, Turkey	A103	PI165064	3.67ab
Smallage, Turkey	A104	PI167075	3.33abc
Celeriac, Turkey	A105	PI167214	4.00a
Smallage, Turkey	A106	PI168995	3.33abc
Smallage, Turkey	A107	PI168996	3.67ab
Smallage, Turkey	A108	PI168997	4.00a
Smallage, Turkey	A109	PI168998	3.67ab
Smallage, Turkey	A110	PI168999	3.67ab
Smallage, Turkey	A111	PI169000	4.00a
Celeriac, Turkey	A112	PI169001	4.00a
Smallage, Turkey	A113	PI169002	3.33abc
Celeriac, Turkey	A114	PI169003	3.33abc
Celeriac, Turkey	A116	PI169005	3.67ab
Celeriac, Turkey	A117	PI169006	4.00a
Smallage, Turkey	A119	PI169008	3.67ab
Smallage, Turkey	A120	PI170031	3.67ab
Celeriac, Turkey	A121	PI171498	3.67ab
Celeriac, Turkey	A122	PI171499	4.00a
Smallage, Turkey	A124	PI172725	4.00a
Celeriac, Turkey	A125	PI174054	3.67ab
Celeriac, Turkey	A126	PI176417	3.67ab
Celeriac, Turkey	A127	PI176419	3.67ab
Celeriac, Turkey	A128	PI176869	3.00bc
Smallage, Turkey	A129	PI177255	3.67ab
Smallage, Turkey	A130	PI177266	3.33abc
Celeriac, Turkey	A131	PI178830	4.00a
Smallage, Turkey	A132	PI178834	4.00a
Celery, 'Golden Self Blanching'	A133	PI179171	3.33abc
Smallage, Turkey	A134	PI181714	3.67ab
Smallage, Egypt	A135	PI183210	3.33abc
Celeriac, Ethiopia	A136	PI193454	4.00a
Smallage, Turkey	A138	PI204557	4.00a
Celeriac, Turkey	A139	PI206940	3.33abc
Celeriac, Switzerland	A140	PI246333	3.33abc
Smallage, Iran	A141	PI254539	3.33abc
Smallage, Thailand	A142	PI257227	3.67ab
Smallage, Thailand	A143	PI257228	3.33abc
Smallage, Turkey	A144	PI261001	3.33abc
Celeriac, Belgium	A145	PI261756	4.00a
Celeriac, Austria	A146	PI261810	3.67ab
Celeriac, 'Apfel'	A147	—	4.00a
Celeriac, 'Alabaster'	A148	—	3.67ab
Celeriac, 'Cera'	A149	—	4.00a
Celeriac, 'Dresdner Market'	A150	—	4.00a
Celeriac, 'Eureka'	A151	—	4.00a
Celeriac, 'Nerez'	A153	—	3.67ab
Celeriac, 'Weiner Market'	A156	—	3.33abc
Celeriac, 'Balder'	A157	—	4.00a
Celeriac, 'Marble Ball', USA	A158	—	3.67ab
<i>A. prostratum</i> , South Africa	A161	—	3.33abc
<i>A. leptophyllum</i> , Australia	A162	—	0.00e
Celeriac, East Germany	A168	—	4.00a
Smallage, East Germany	A171	—	3.33abc
Smallage, East Germany	A172	—	3.67ab
Celeriac, 'Non Plus Ultra'	A173	PI200069	3.67ab
Celery, Italy	A175	PI200070	3.00bc
Celery, Italy	A176	PI200086	3.33abc

Table 1. Continued

Description	Accession #	USDA PI # ^a	Leaf-mining index ^b
Celery, Italy	A179	PI200203	3.67ab
Celery, Italy	A180	PI200239	3.33abc
Celery, Italy	A181	PI200312	3.00bc
Celery, 'Hopkins Finlander'	A187	—	3.67ab
Celery, 'New Dwarf White'	A188	—	3.33abc
Celery, 'Asmer Celebrity'	A189	—	3.67ab
Celery, MSU (k-4)	A190	—	3.00bc
Celery, MSU 83-605	A199	—	4.00a
Celery, MSU 85-606	A201	—	3.33abc
Celery, MSU 68-37	A202	—	3.33abc
Celery, 'UC1'	A203	—	3.67ab
Smallage, 'Couper de Dinant'	A205	—	3.67ab
Celery, 'D'Eln Race Isel'	A206	—	3.33abc
Celery, 'Grand Dore' race 'Super Dora'	A207	—	4.00a
Celery, 'Le Page Aris'	A208	—	3.67ab
Smallage, 'Lepage' race 'Istra'	A209	—	4.00a
Celeriac, 'Naxos'	A210	—	4.00a
Celeriac, 'Neve'	A211	—	3.50abc
Celery, 'Verdon'	A212	—	3.00bc
Celery, 'Triumph'	A213	—	3.33abc
Celery, 'Lathom Selfire'	A214	—	3.00bc
Celeriac, 'Nemona'	A215	—	3.33abc
Smallage, 'Afina'	A216	—	3.00bc
Celeriac, 'Alba'	A217	—	4.00a
Celeriac, 'Monarch'	A218	—	4.00a
Celeriac, 'Brazsky 'Obrovsky'	A219	—	3.67ab
Celeriac, 'Maxim'	A220	—	3.67ab
Celeriac, 'Arion'	A221	—	4.00a
Celeriac, 'Apia'	A222	—	4.00a
Smallage, China	A226	PI478315	3.33abc
<i>A. prostratum</i> , Australia	A230	—	2.00d

Data from August 1985 during peak leafminer populations. Celeriac, *A. graveolens* var. *rapaceum*; smallage, *A. graveolens* var. *secalinum*.

^a U.S. Department of Agriculture Plant Introduction Number (as available).

^b 0, 1, 2, 3, and 4; 0, 1–25, 26–50, 51–75, and >75% of the leaves per plant with at least one live larva present, respectively. Means followed by the same letter are not significantly different ($P > 0.05$, Student-Newman-Keuls test [SAS Institute 1985]).

populations on a less preferred variety if given no choice. Thus, the no-choice laboratory experiments were needed to address the potential suitability of *Apium* accessions for leafminer survival and development.

Laboratory Experiments. *A. prostratum* (A230) was the only accession to exhibit probable antixenosis. No feeding or oviposition were observed on this variety in the laboratory (Table 2), but limited oviposition occurred in the field (Table 1). Although the basis for the observed resistance has not been identified, the lack of feeding or oviposition punctures in the lab suggests that this accession may contain repellent chemicals or lack stimulants. Adult leafminers were observed to land on the plants and probe first with their mouthparts and then with their ovipositors (which have basiconic chemoreceptors [Knodel-Montz & Poe 1982]), after which they rapidly left the leaf surface. No attempts to penetrate the leaf with an ovipositor were ob-

served, suggesting that differences in leaf toughness were not a primary influence on rejection by *L. trifolii*. However, because some mining was observed in this accession in the field, a greater genetic variability in field populations of leafminers compared with our laboratory colony may reduce the usefulness of this accession in commercial situations.

Substantial differences in host suitability were observed between the other accessions we evaluated. Surprisingly, even though leafminers demonstrated a significantly ($F = 6.59$; $df = 7, 72$; $P < 0.001$) greater acceptance of some accessions for adult feeding and oviposition, only *A. prostratum* (A230), which showed no mining, generated significant differences ($F = 7.62$; $df = 7, 72$; $P < 0.001$) in numbers of mines from any other accession (Table 2). However, significantly ($F = 10.72$; $df = 7, 72$; $P < 0.001$) fewer leafminers successfully pupated and emerged as adults if reared on (A230), *A. chilense* or the hybrids (A41) × (A73) or (A41) × (A160). Thus, antibiosis is the basis for resistance in these accessions. None of the pupae reared from any plant species appeared to be deformed or abnormal. The increase in mortality for leafminers developing on the hybrids compared with the parental accessions not only suggests that the antibiotic response is a dominant trait, but that the response is magnified in the hybrids as a heterotic response. Thus, hybrid vigor may be a valuable breeding tool for manipulating celery resistance to insects.

No significant differences ($F = 0.61$; $df = 6, 62$; $P > 0.7$) between accessions were observed for the time required for development from egg to pupa (range, 7.7–8.0 d) or for the ratio of punctures to mines (range, 1.4–2.7). The similarity in developmental rates is consistent with previous reports for *Liriomyza* species among vegetable species (Via 1984b, Minkenburg & van Lenteren 1986), among tomato varieties (Webb & Smith 1969), and among chrysanthemum varieties (Webb & Smith 1969), but it contrasts with variability in developmental times on weeds (Smith & Hardman 1986). Lack of differences between accessions in the ratio of punctures to mines suggests that in no-choice situations, these accessions were equally acceptable for oviposition. However, this conclusion should be interpreted with caution, as Hussey & Gurney (1962) and Parrella et al. (1983) reported that the ratio of punctures to viable eggs may not be a valid measure of host preference unless calculated over nearly the entire lifespan of the adult female.

Resistant accessions with antibiotic or antixenotic effects have considerable potential for slowing the growth rates of pest populations (Kennedy et al. 1987). Resistance based on antixenosis would be desirable because even the photosynthetic losses caused by adult feeding and oviposition would be reduced (Trumble et al. 1985). Therefore, attempts to hybridize *A. prostratum* (A230) with 'Tall Utah' 5270 HK are currently in progress. Whether or not

Table 2. Influence of *Apium* accession on *L. trifolii* oviposition, development, and survival

Celery accession ^a	No. feeding punctures per plant	No. per plant			Ratio per plant	
		Mines	Pupae	Adults	Pupae/mines	Adults/pupae
(A209) 'Lepage race Istra'	87.6a	37.2a	34.0a	26.6a	0.95a	0.78a
(A41) 'Tall Utah' 5270 HK	73.4ab	35.1a	33.4a	28.1a	1.00a	0.83a
(A160) <i>A. panul</i>	68.6ab	35.1a	31.3a	27.2a	1.06a	0.88a
(A161) <i>A. prostratum</i>	47.7ab	37.1a	38.5a	23.8a	1.03a	0.60b
(A73) <i>A. chilense</i>	34.0bc	24.5a	19.4b	16.7ab	0.80ab	0.90a
(A41) × (A73)	67.7ab	26.9a	17.9b	7.7bc	0.65bc	0.50b
(A41) × ((A160)	35.3bc	23.7a	11.2bc	6.3bc	0.53c	0.56b
(A230) <i>A. prostratum</i>	0.0d	0.0b	0.0c	0.0c	— ^b	— ^b

Means within columns followed by the same letter are not significantly different ($P > 0.05$, Student-Newman-Keuls test [SAS Institute 1985]).

^a University of California Davis, Department of Vegetable Crops accession numbers.

^b Division by zero precludes analysis.

this proves possible, the antibiosis-based resistance will be pursued. Because *L. trifolii* is broadly polyphagous (Minkenberg & van Lenteren 1986), an antibiosis-based resistance for the larvae may provide better regional population reductions than antixenosis or nonpreference approaches, which could foster destructive intercrop movements.

In our experiments, if fitness of the leafminer offspring from the partially resistant plants is conservatively assumed to be equivalent to that of offspring from control plants, the reduction in population development resulting from lower ratios of pupae/mines and adults/pupae would range from 61 to 64% (after correction for mortality on susceptible celery [A41]). If used in conjunction with key parasite species, which can cause up to 90% mortality of the larval leafminer populations in celery (Trumble & Nakakihara 1983), considerable potential exists for substantial reductions in pesticide use.

The commercial success of this project will be based upon the fertilities of *A. graveolens* (A41) × *A. chilense* (A73) and *A. graveolens* (A41) × *A. panul* (A160), which have been low and have prevented us from obtaining F_2 seeds. This was because of the action of chromosomal rearrangements present in the wild species (C.F.Q., unpublished). However, chromosomal associations in the form of bivalents took place between the genomes of the different species and backcross seed from the first hybrid with *A. graveolens*. Ideally, plants developing from these seeds should be evaluated for leafminer resistance and for isozyme marker segregations to determine whether genetic recombination occurs between the different genomes.

Further selection of parental plants from the wild species *A. panul* and *A. chilense* for high fertility and absence of chromosomal aberrations would be desirable in order to repeat the hybridizations. The resulting hybrids then should be examined for leafminer resistance to determine if the resistant trait is dominant or recessive, and for the presence of undesirable chemicals. Chemicals such as the psoralens can be toxic to mammals, and breeding for resistance based on these compounds

would not have practical value. This information will provide the background data required before undertaking a large-scale celery breeding program for leafminer resistance.

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