Experimental Hosts of the Beet Leafhopper-Transmitted Virescence Agent

D. A. GOLINO, Research Plant Pathologist, USDA-ARS, Department of Plant Pathology, University of California, Davis, and G. N. OLDFIELD, Lecturer, and D. J. GUMPF, Professor, Department of Plant Pathology, University of California, Riverside 92521

ABSTRACT

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The vector *Circulifer tenellus* was used to inoculate 60 species of plants with the beet leafhopper-transmitted virescence agent (BLTVA). A wide range of host reactions was seen in 43 species, including floral gigantism, host induction response, internode elongation, internode shortening, leaf deformation, leaf mottling, proliferation, stunting, tip necrosis, virescence, wilting, and yellowing. No nonsymptomatic hosts were found, but 17 plant species did not develop symptoms of infection after exposure to inoculative leafhoppers; this included all the monocots tested. A number of plants that have been reported as hosts of economically important MLO diseases also proved to be hosts of BLTVA. In seven host species, flowering was induced in plants grown under environmental conditions that would normally be noninductive for flowering.

Beet leafhopper-transmitted virescence agent (BLTVA), a mycoplasmalike organism (MLO) (10), was first described in the context of its ecological association with the citrus stubborn agent, *Spiroplasma citri* Saglio et al (19), in infected Madagascar periwinkle. Early work with BLTVA included some preliminary host range data. *Arabidopsis thaliana* (L.) Heynh., *Brassica geniculata* (Desf.) J. Ball, *B. oleracea* L., *Raphanus sativus* L., *Sisymbrium irio* L., and a *Phlox* species were reported as hosts (12,19,20). The transmission characteristics of the agent have been established (10). In a study of the biology of BLTVA, it was discovered that flowering could be induced in selected infected hosts, even when environmental requirements for the induction of flowering had not been satisfied (11). This induction of flowering, designated the host induction response (HIR), is possibly related either to the disruption of the host's normal gibberellic acid (GA) metabolism or to actual production by the MLO of GA or its precursors.

To further define the host range of this unique MLO, a large number of additional plant species were evaluated as potential hosts. An effort was made to select plants that might be useful on the basis of any one of three criteria: plants that might be economically or ecologically important in the natural biology of the organism (3,6,7,22); plants that were well-characterized as hosts of other MLOs, thereby providing a basis for symptom comparison (4,5,9,14,15,18); and plants that had well-documented flowering responses after applications of exogenous GA (23) and thus might be expected to show the HIR.

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MATERIALS AND METHODS

The pathogen. A well-characterized line of BLTVA, FC-83-13, (10) was used for all experiments. It has been maintained in our laboratory since the fall of 1983 when it was transmitted to a young periwinkle plant by a single beet leafhopper collected from Buena Vista, Kern County, California. The same line of BLTVA was used for leafhopper transmission studies (10) and shown to cause the HIR in selected hosts (11). It has been maintained in our greenhouses in either periwinkle (*Catharanthus roseus* (L.) G. Don. 'Little Pinkie') or radish plants (*Raphanus sativus* 'Scarlet Turnip White Tipped' or 'Summer Cross Hybrid'). Normal passage is through the leafhopper vector *Circulifer tenellus* (Baker); only rarely, grafted periwinkle is used as a source of the line of BLTVA.

Plants and insects. Most plants were grown from seed in a greenhouse fumigated biweekly with 2,2-dichlorovinyl dimethyl phosphate (DDVP). The exceptions were *Armoracia rusticana* P. Gaertn., B. Mey., & Scherb., *Ranunculus* hybrids, and *Fragaria vesca* L. 'Sequoia,' which were grown from nursery stock and purchased locally. When nursery stock was used, at least six clean control plants were reared to maturity so the material could be visually assessed for the presence of pathogens. Potential hosts were 4–8 cm high when used for experiments. The species and cultivars tested are listed in Table 1 and arranged by family groupings. Some hosts that had been previously identified as BLTVA-infected were retested, since previous work was accomplished with other lines of the MLO.

C. tenellus were reared on sugar beet (*Beta vulgaris* L. 'VH510'). Leafhoppers from the rearing colonies were fed at least monthly on healthy periwinkle plants to ensure that the population remained free from phytopathogens for which periwinkle is an indicator plant (18). Colonies were maintained in a glasshouse at 20–30 C under a light:dark regimen of 16:8.

Inoculation. BLTVA-inoculative leafhoppers were produced by allowing groups of several hundred leafhoppers to oviposit on BLTVA-infected radish plants. The adults were removed after about 2 wk. Within 6–8 wk, the highly inoculative progeny could be used to infect potential hosts.

The inoculation test for each species consisted of a group of 12 young plants. All were covered in a light cylindrical cage (21). Nine plants were each fed upon by 10 inoculative adult leafhoppers produced as described above; three plants each received 10 noninoculative leafhoppers. Leafhoppers were allowed to feed for 1 wk, then plants were fumigated with DDVP and placed in a separate greenhouse for observation. Each time a group of potential hosts was tested, inoculative insects were also placed on three young periwinkle plants, a susceptible host frequently used as an assay plant for various MLOs. If the periwinkle indicator eventually developed symptoms, the inoculativity of the larger group of insects fed on the potential new host could be assured; when the positive control periwinkle failed to develop symptoms, the entire experiment was repeated.

Any plant that developed symptoms of BLTVA infection was observed and photographed over a period of several months. When greenhouse space was available, noninoculative *C. tenellus* were fed on one or more symptomatic plants for 2 days, held on sugar beet for a 3-wk latent period, and then transferred in groups of 10 to indicator periwinkle. This backpassage procedure was also attempted from a number of plant species that did not develop symptoms in an effort to ascertain whether BLTVA could infect plants without producing symptoms.

RESULTS

Of the 60 species of plants we tested as potential experimental hosts of BLTVA, 43 developed distinct symptoms of disease after inoculation (Table 1). Backpassage experiments confirmed the presence of BLTVA in 30 of these species. In all cases when it was attempted, backpassage from symptomatic hosts to periwinkle was possible. Among the 17 species of plants that failed to show any symptoms of infection after inoculation, backpassage experiments were performed on *Allium fistulosum* L., *Avena sativa* L., *Hordeum vulgare* L., *Triticum aestivum* L., and *Zea mays* L. None was found to harbor BLTVA, and therefore no nonsymptomatic hosts were identified.

A wide range of host reactions was seen in BLTVA-infected plants (Table 1), including floral virescence and phyllody (always observed together) (Figs. 1A–E and 2A, B, D, and E); floral gigantism (Figs. 1B and 2B); floral proliferation (Fig. 2A); the HIR (Fig. 2C); internode elongation (Figs. 1E and 2B and E); internode shortening (Fig. 1A); leaf deformation, leaf mottling, and proliferation of adventitious buds (Figs. 1E and 2A and E); stunting (Fig. 1A); and tip necrosis, wilting, and yellowing (Fig. 2D).

None of the monocots tested developed symptoms of infection, and the agent was not recovered from plants during backpassage experiments with leafhoppers. Many dicots were susceptible to infection, and there was no

Table 1. Reactions of plant species to inoculation with the beet leafhopper-transmitted virescence agent (BLTVA) isolate FC-83-13

Family Genus, species, cultivar[a]	Host reactions[b]
APOCYNACEAE	
Catharanthus roseus (L.) G. Don 'Little Pinkie'*	FV,FP,P
ASTERACEAE	
Bellis perennis L.	NS
Calendula officinalis L. 'Yellow Gem'*	FP,FV,Y
Callistephus chinensis (L.) Nees 'American Branching'*	FP,FV,IS,LM,TN,Y
Cichorium intybus L.	NS
Coreopsis tinctoria Nutt. 'Annual Dwarf'*	FP,FV,P
Gerbera jamesonii Bolus ex Hook. f.	NS
Helichrysum bracteatum (Venten.) Andr.	NS
Lactuca sativa L. 'Oakleaf'*	FP,FV
Rudbeckia hirta L.	FP,FV,P
Tagetes L. hybrid 'Sparky Dwarf'	FV,IS,LM,P,ST,Y
Zinnia elegans Jacq.	NS
CARYOPHYLLACEAE	
Dianthus caryophyllus L. 'Red Wonder'	NS
CHENOPODIACEAE	
Spinacia oleracea L. 'Melody'*	IE,Y
CRUCIFERAE	
Armoracia rusticana P. Gaertn., B. Mey., & Scherb.	FV,HIR
Aurinia saxatilis (L.) Desv. 'Gold Dust'*	LM,ST,W,Y
Brassica campestris L. (field-collected seed)	FP,FV,P
B. geniculata (Desf.) J. Ball* (field-collected seed)	FV,P
B. napus L. 'Laurentia'*	FV
B. oleracea L. 'De Cicco'*	FP,FV
B. oleracea 'Dwarf Blue Curled'*	FP,FV,P
B. oleracea 'Ornamental'*	FV
B. oleracea 'Snowball'	FV
B. rapa L. 'Michihli'*	FP,FV,HIR
B. rapa 'Purple Globe'*	FP,FV,HIR
Eruca vesicaria (L.) Cav. 'Roquette'*	FV
Iberis umbellata L. 'Fairy Mix'*	FG,FP,FV,IE,P
Raphanus sativus L. 'Scarlet Turnip White Tipped'*	FV,HIR
R. sativus 'Summer Cross Hybrid'*	FV,HIR
CUCURBITACEAE	
Cucumis sativus L. 'Spacemaker'*	FG,FV,P
GRAMINEAE	
Avena sativa L. 'Montezuma'	NS
Hordeum vulgare L. 'CM67'	NS
Triticum aestivum L. 'Anza'	NS
Zea mays L. 'Early Sunglow'	NS
LEGUMINOSAE	
Arachis hypogaea L. 'Jumbo Virginia'*	FP,FV,IS,P,Y
Phaseolus vulgaris L. 'Contender'	FP,FV,P
Pisum sativum L. 'Little Marvel Improved'	FV,IS,P,ST
Trifolium pratense L. 'Red Clover'	NS
Vigna unguiculata (L.) Walp. 'California Blackeye'*	FP,FV,IS,P
LILIACEAE	
Allium fistulosum L. 'Green Bunching'	NS
A. fistulosum 'Sweet Spanish'	NS
MALVACEAE	
Alcea rosea L. 'Charter's Double'	FV
PAPAVERACEAE	
Papaver nudicaule L. 'Champagne Bubbles'	NS
PLANTAGINACEAE	
Plantago major L.	FG,FP,FV
PORTULACACEAE	
Portulaca grandiflora Hook. 'Magic Carpet'*	FG,FP,FV,IS,P,ST
PRIMULACEAE	
Primula × *polyantha*	IS,ST,W,Y
RANUNCULACEAE	
Anemone coronaria L. 'Saint Brigid'	FV,ST,W,Y
Aquilegia L. hybrid	FP,FV,IS,P,Y
Consolida regalis S. F. Gray*	FP,FV,IS,ST,TN,Y
Delphinium hybrid 'Pacific Giants'*	FP,FV,IS
Nigella damascena L. 'Love-in-a-Mist'*	FP,FV,IE
Ranunculus asiaticus L. 'Persian'	FV,ST,W,Y
ROSACEAE	
Fragaria vesca L. 'Alpine'	NS
F. vesca 'Sequoia'	NS
SCROPHULARIACEAE	
Antirrhinum majus L.	NS
SOLANACEAE	
Capsicum annuum L. 'California Wonder'	FV,IS,ST,Y
Lycospericon esculentum Mill. 'Pixie'*	FG,FP,ST,Y
L. esculentum 'Ace VF Resistant'	FG,FP,LD,LM,ST,TN,Y
Petunia hybrid 'Apple Blossom'*	IS,FV
Solanum melongena L. 'Black Beauty'	NS
Schizanthus Ruíz & Pavón hybrid	FV,P
TROPAEOLACEAE	
Tropaelum majus L. 'Golden Gleam'*	FV,IS,P,ST,TN,W,Y
UMBELLIFERAE	
Anethum graveolens L. 'Bouquet'*	FP,FV,HIR,IE
A. graveolens 'Burpee's 6144'	FP,FV,HIR,IE
Apium graveolens L. 'Fordhook'*	HIR,IE,Y
Coriandrum sativum L.*	FV,TN,W,Y
Daucus carota L. 'Red Cored Chantenay'*	FV,HIR,IS,TN,Y
Petroselinum crispum (Mill.) Nyman ex A.W. Hill 'Italian'*	FV,HIR,IE
VIOLACEAE	
Viola cornuta L.	NS

[a]An asterisk indicates plants from which BLTVA could be recovered using the vector, *Circulifer tenellus*, and backpassaged to the indicator, periwinkle (*Catharanthus roseus*).

[b]FG = floral gigantism, FP = floral proliferation, FV = floral virescence and phyllody, HIR = host induction response, IE = internode elongation, IS = internode shortening, LD = leaf deformation, LM = leaf mottling, NS = no symptoms, P = proliferation of adventitious buds, ST = stunting, TN = tip necrosis, W = wilting, Y = foliar yellowing.

apparent taxonomic relationship among the dicots that failed to develop symptoms. Most dicots proved susceptible to infection after repeated inoculation.

The time required for symptom development varied greatly among hosts. Symptoms were observed in as few as 4 wk post inoculation in periwinkle. By contrast, cucumber did not develop symptoms until 12–14 wk after infection. Cucumber plants were held this long because backpassage experiments performed 6–8 wk post inoculation indicated that cucumber harbored BLTVA. Until this time, the plants flowered profusely and appeared normal. Several crucifers, e.g., *Armoracia rusticana, Brassica geniculata, B. oleracea, B. rapa* L., and *Raphanus sativus*, showed no foliar symptoms; infected and healthy plants of these species were indistinguishable until flowering occurred, at which time floral symptoms became evident. Generally, symptoms could be seen within 6–8 wk after inoculation, and only a few species of special interest were held for more than 4 mo post inoculation.

A few species responded with severe symptoms. A general stunting and yellowing was followed by leaf necrosis, wilting, and death within a few weeks after the first symptoms developed in *Anemone coronaria* L., *Aurinia saxatilis* (L.) Desv., *Consolida regalis* S. F. Gray, *Coriandrum sativum* L., and *Primula* × *polyantha*. The effect of infection on flowering in *A. saxatilis* and *P.* × *polyantha* could not be ascertained because the plants did not survive long enough to bloom. In those cases where more than one cultivar of a plant species was tested, a consistent result (host or nonhost) was obtained. However, symptoms in different susceptible cultivars of a species were not always identical; *Lycopersicon esculentum* Mill. was a good example (Table 1).

Of particular note was that BLTVA was able to infect a number of hosts that have been reported in the past as important hosts of other MLOs. China aster (*Callistephus chinensis* (L.) Nees) developed symptoms similar to those described for the aster yellows MLO in the same host (5) (Fig. 2D). Both cultivars of tomato tested (Table 1) developed a big bud symptom (Fig. 1B and C) much like the tomato big bud disease reported as an economic problem in tomato in areas as diverse as Israel, North America, and Australia (8,13). BLTVA-infected nasturtium (*Tropaeolum majus* L.) strongly resembles illustrations of nasturtium infected by clover phyllody MLO (2). The symptoms produced by BLTVA infection of *Plantago major* L. were quite distinct from those produced in our greenhouses by inoculation of *P. major* with lines of either dwarf aster yellows (DAY) MLO or severe aster yellows (SAY) MLO provided by A. H. Purcell (University of California, Berkeley). When inoculated and observed under identical conditions in our greenhouses, plants infected with either DAY-MLO or SAY-MLO were stunted and chlorotic with leaf deformation and tip necrosis. The BLTVA-infected *P. major* shared symptoms of floral proliferation and virescence with the DAY- and SAY-infected plants but showed no foliar symptoms or reduction in vigor.

The HIR was observed in seven species of plants (Table 2). These included both long-day plants grown under short days, such as *Raphanus sativus* 'Scarlet Turnip White Tipped' (Fig. 2C), and plants that normally require cold to flower, such as *Apium graveolens* L. (23). Many months were required before infected *Armoracia rusticana* bloomed after inoculation.

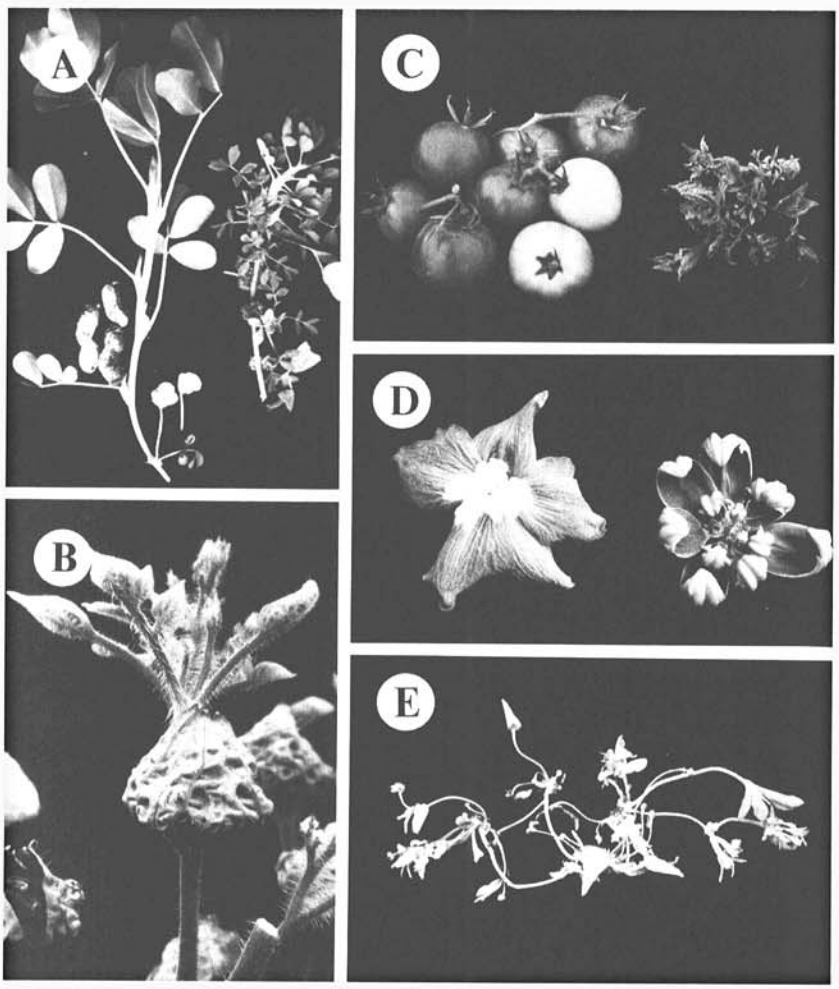

Fig. 1. Symptoms of infection by beet leafhopper-transmitted virescence agent: **(A)** Stunting and floral witches'-broom on infected peanut (right). **(B)** Big bud symptom on infected tomato blossom with leaflike development of stamens and pistils. **(C)** Fruit harvested from healthy (left) and infected tomato. **(D)** Phyllody of infected delphinium petals (left). **(E)** Portion of a blossom of infected *Coreopsis* showing the proliferation of secondary buds from the capitulum of the primary flower.

DISCUSSION

BLTVA can be readily transmitted to many dicots by *C. tenellus* under laboratory conditions, as shown by symptom expression or backpassage to a susceptible host. None of the monocots that were tested developed symptoms of infection, and backpassage from them was unsuccessful. Other MLOs are known to have host ranges that include both dicots and monocots (1,18), so additional experimental work is required to clearly establish this apparent difference.

Transmission in the laboratory involved holding leafhoppers in cages where they must feed on test plants in order to survive. Under these conditions, plants that would not normally be exposed to the agent can be infected. It is therefore unlikely that BLTVA would have an equally extensive host range under natural conditions in California.

The HIR has been shown in several plant species known to be sensitive to GA (11,23). We were able to document the HIR in seven species of plants; it is possible that the HIR occurs in additional species, including some of the other BLTVA-infected hosts in this study. It is also possible that some hosts were tested during a time of year when HIR would be masked by inductive environmental conditions. Therefore, a plant in which the HIR was not observed

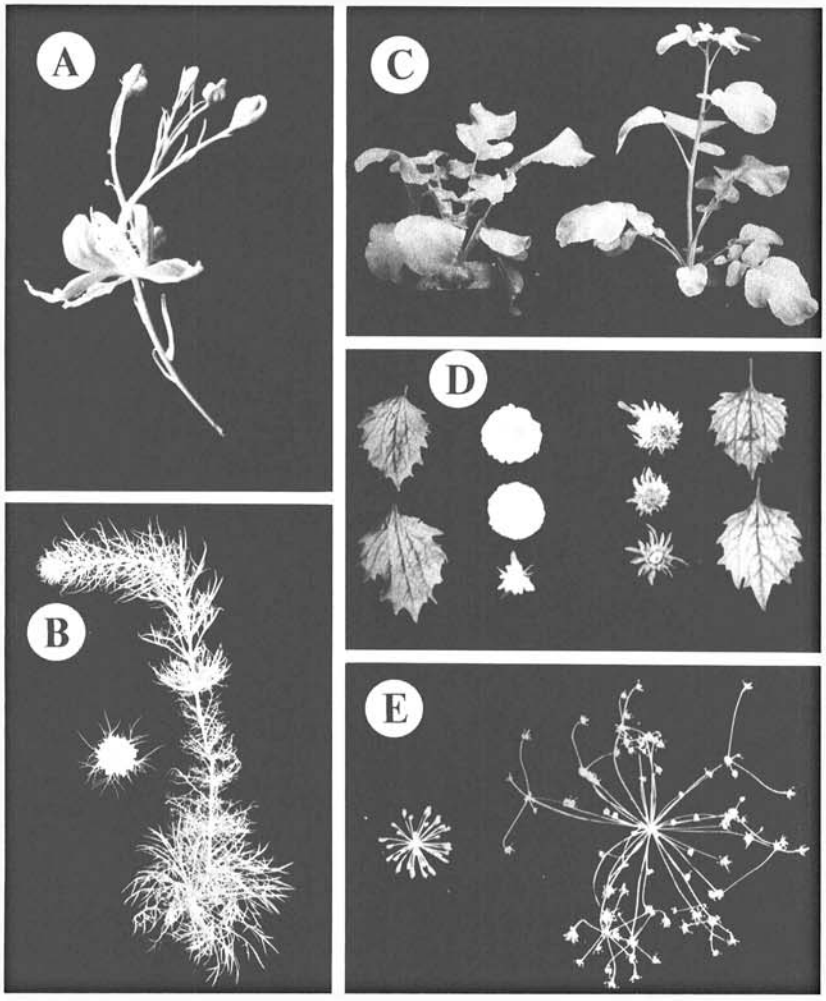

Fig. 2. Symptoms of beet leafhopper-transmitted virescence agent in various host plants: **(A)** Delphinium flower with virescence and secondary flowers developing from carpels. **(B)** Healthy blossom of *Nigella* (left) next to an infected blossom showing indeterminate stem elongation as well as phyllody. **(C)** Host induction response resulting in flowering of infected radish (right). **(D)** Healthy (left) and infected leaves and flowers of China aster (*Callistephus chinensis*). **(E)** Healthy (left) and infected umbellets of dill.

Table 2. Plant species observed to respond to infection by the beet leafhopper-transmitted virescence agent with the host induction response (HIR)

Plant species	Cultivar	Test number	Percent HIR[a]
Anethum graveolens	Burpee's 6144	34	78
Apium graveolens	Fordhook	33	96
Armoracia rusticana	Unknown	9	22
Brassica rapa	Purple Globe	9	33
	Michihli	9	100
Daucus carota	Red Cored Chantenay	18	61
Petroselinum crispum	Italian	18	33
Raphanus sativus	Scarlet Turnip White Tipped	45	80
	Summer Cross Hybrid	18	88

[a]Calculated by subtracting the percentage of control plants flowering from the percentage of inoculated plants flowering.

may potentially respond under other carefully selected environmental conditions, i.e., the HIR might not be noted in a plant that flowers in summer regardless of other factors, but in winter, the effects of BLTVA infection would be pronounced (11). A specific example in this study was lettuce. Despite repeated tests conducted during short days under which lettuce should not flower, both inoculated test plants and the healthy controls flowered. We believe that the stress of caging, insect feeding, and fumigation may have triggered bolting, which would have obscured the HIR in lettuce if it did occur. If further research is done on the mechanism of this phenomenon, a wide range of hosts in which to study the HIR is available.

Two cultivars of radish, Scarlet Turnip White Tipped and Summer Cross Hybrid, both tested positive for the HIR. Scarlet Turnip White Tipped flowers occasionally under greenhouse conditions in winter even when uninfected. Summer Cross Hybrid, a biennial long, white, daikon-type radish, does not flower during either winter or summer under greenhouse conditions (23). It may be advantageous for future research on the HIR to use this cultivar of radish in which the environmental barriers for induction of flowering are higher.

In addition to the HIR, a number of other symptoms were seen that might also be attributed to increased levels of GA or some other hormone. Individual flowers of BLTVA-infected *Nigella damascena* L. were not only virescent but showed extensive stem elongation and an indeterminate growth resulting in a long feathery flower (Fig. 2B). Flower buds of *Coreopsis tinctoria* Nutt. were initiated along the stem at sites where flowers would not normally occur (Fig. 1E). Proliferation of flower buds from axillary meristems within individual flowers was also seen in other species, including *Delphinium* hybrids and *Anethum graveolens* L. (Fig. 2A and E).

Current knowledge of the taxonomic relationships among the MLOs is extremely limited because they have not yet been cultured. This has greatly handicapped efforts at genetic and biochemical characterization of the MLOs (15). High-quality polyclonal antisera is difficult to obtain. Progress with the production of monoclonal antibodies (17) and molecular DNA probes (16) to these agents may clarify the relationships among various described MLOs. At this time, host range data and vector relationships remain an important component of the descriptive data required to characterize these organisms (18). BLTVA causes symptoms similar or identical to those caused in several hosts by other MLOs. Whether this similarity of symptoms implies any relatedness between BLTVA and other MLOs is unknown.

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