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H I L G A R D I A

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INFECTION OF PERENNIAL DELPHINIUMS BY CALIFORNIA-ASTER-YELLOWS VIRUS[1]

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INTRODUCTION

SEVERAL OBSCURE diseases attack garden varieties of perennial delphiniums (hybrids and horticultural varieties of several species of *Delphinium*) and cause losses to seed companies, nurserymen, and growers. One of these diseases is particularly troublesome, sometimes causing delphiniums grown from seed to fail totally the second year. Some of the choicest seeds, requiring hand-pollination and bagging, are grown in California; and often these hybrid seeds, also selected for mildew resistance, are lost owing to this disease. Because the symptoms resemble those of California aster yellows on other host plants, an investigation was undertaken to determine whether this disease is caused by the virus of California aster yellows.

In the course of the work on this disease, several other delphinium virus diseases and troubles resembling viroses were investigated. The reports of these investigations have been divided into six papers. The present paper is confined to the work with California aster yellows on perennial delphiniums. Experiments with two other naturally occurring viroses of perennial delphiniums are reported in the other papers of this issue (*18, 22*).[3] The attempts to infect perennial delphiniums experimentally with other viruses are reported in a fourth paper (*20*). Two leaf variegations of perennial delphiniums resembling viroses but not infectious were encountered; these are reported in a fifth paper (*19*). Several of the virus diseases attacking perennial delphiniums affect also annual delphiniums, or larkspur (*Delphinium Ajacis*); the experiments with this host plant are published in a sixth paper (*21*).

[1] Received for publication May 16, 1941.

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[3] Italic figures in parentheses refer to "Literature Cited" at the end of this paper.

California aster yellows is a serious disease of aster and celery, and affects also lettuce (*13*), carrots, parsley, and parsnip (*14*), and many ornamentals (*23*). Except in a preliminary note (25) based on this investigation, however, it has not previously been reported on delphinium. Nevertheless, the symptoms described by several investigators in other states indicate that they may have been dealing with this disease.

In 1927 Linford (*33, 34*) reported 50 per cent of yellows (cause undetermined) on tall perennial delphinium at Logan, Utah; he evidently suspected the disease to be aster yellows but stated that delphiniums were not known to be susceptible to that disease, and conducted no tests.

In 1933 Hungerford (*35*) reported a new virus disease on delphinium at Moscow and Boise Valley, Idaho, and suggested "witches'-broom" as a common name.

Orton (*10*) reported a new virus disease of delphiniums in the Northwest called "greens," which stunts the plants and makes them produce nothing but dwarfed green flowers.

Heald and Burnett (*6*) described a virus disease of perennial delphinium in the State of Washington and applied the name "stunt" to the disease.

A more complete discussion of the same delphinium disease in that state was published by Burnett (*2*), again under the designation "stunt." Several references on the distribution of "stunt" (virus) of delphinium in the states of Washington and New York have appeared in the *Plant Disease Reporter* (*36, 37, 38*).

In the present investigation, the symptoms of the disease on naturally infected delphiniums were compared with those on delphiniums experimentally infected with California aster yellows. Field investigations were undertaken to determine the most important vectors of the virus of delphiniums. Attempts were made to recover the virus from naturally infected delphiniums by the mountain leafhopper, *Thamnotettix montanus* Van D.; the geminate leafhopper, *T. geminatus* Van D.; the short-winged aster leafhopper, *Macrosteles divisus* (Uhl.) (=*Cicadula divisa*), and the long-winged aster leafhopper, a physiological race or variety of the same species (*17*); and to transfer it to healthy aster and celery plants. Attempts were made to infect healthy delphiniums grown from seeds with the virus obtained from diseased aster and celery plants by the four vectors and to recover the virus from the infected delphiniums and transfer it back to healthy aster and celery plants by previously noninfective leafhoppers. The delphinium varieties and hybrids experimentally infected, the incubation period of the disease in delphiniums, and the weed reservoirs of the virus in and near delphinum fields were also investigated.

METHODS

Rhubarb (*Rheum Rhaponticum*) is immune to California aster yellows and was found to be a favorable breeding plant of the geminate leafhopper. Adults collected on delphiniums in the field were confined in cages enclosing rhubarb plants in which they oviposited. The adults were removed from the cages before the nymphs hatched from the eggs. The males reared during the nymphal stages on rhubarb plants, as well as adults of the later generations, were frequently transferred to celery plants, but caused no infection. Males were used instead of females, to avoid egg deposition.

The production of noninfective short-winged aster leafhoppers (reared on mildew-resistant Sacramento barley immune to aster yellows), mountain leafhoppers, and geminate leafhoppers (the last two reared on healthy celery) have been described in previous papers (*14, 16*). The long-winged aster leafhopper also remained noninfective when reared on Sacramento barley.

SYMPTOMATOLOGY

The description of the symptoms of aster yellows pertaining to the abnormal development of the flower is in general terminology, since no anatomical comparison has been made of the normal and abnormal flower structures.

One of the most conspicuous symptoms of aster yellows on naturally infected delphiniums, when roguing of diseased plants is not practiced, is the dwarfing of some of the plants. A general yellowing of the foliage occurred on the stunted plants. It was not uncommon to find a dense cluster of yellow shoots about 6 inches high which never developed spikes. A closer examination of one of these shoots revealed numerous lateral or axillary shoots (plate 1, *A*) bearing abnormal leaves—instead of 3 lobes or divisions, 2 lobes may be dwarfed, or 1 or 2 lobes may be absent (plate 1, *C*), or the blades may be linear or even seem to be reduced to the midvein with threadlike petioles (plate 1, *A*).

Frequently many slender shoots from 6 to 12 inches or more in height grow from the crown. The petioles are elongated with chlorotic leaves, which may be cupped inward (plate 2, *C, D*). These slender shoots may remain dwarfed until the blossoming period or they may develop slender spikes. It was not unusual to find delphinium plants 3 to 5 feet high with spikes bearing abnormal flowers and with slender, chlorotic shoots, which never developed spikes, at the base of the plant.

Other striking symptoms of aster yellows on naturally and experimentally infected delphiniums were several abnormalities in the de-

velopment of the flowers. Green flower buds (plate 3, *A*) expanded into enlarged green leafy sepals and dwarfed petals (plate 3, *B;* plate 4, *A, B*). The most remarkable peculiarity was the appearance in the normal position of the carpels of structures resembling leaves with green blades and petioles; the petals were dwarfed and surrounded by enlarged green sepals (plate 3, *C;* plate 4, *D, F*). Frequently the sepals, petals, carpels, and stamens were replaced by green leafy structures (plate 3, *D*), and sometimes enormous clusters of these abnormal floral parts developed at the apical region of the spike (plate 2, *B*).

Phyllody, or the transformation of stamens, petals, carpels, or all of the floral parts into leafy structures, is frequently caused by parasites, but other disturbances, such as general effects of soil excesses or overnutrition, may produce similar effects (*5*). Phyllody and virescense, or greening of the flowers, are common symptoms of aster yellows among ornamentals, economic plants, and weeds. In all probability these symptoms described by plant teratologists on many plants are caused by this virus.

A sectorial infection was observed on some delphinium plants in which normal-colored flowers and abnormal flowers with green, leafy sepals and petals occurred on opposite sides of the same spike (plate 2, *A*). Sometimes abnormal flowers with green floral parts were found on the spikes of one or more stalks and apparently normal flowers on the spikes of the remaining stalks. A cluster of apparently normal flowers was present on the apical region and often near the basal region of spikes, with the intermediate or basal region of the spikes bearing filamentous structures (plate 5, *A, B*). Dwarfed flowers with elongated pedicels were found on some spikes (plate 5, *C*). A closer examination of the dwarfed flowers showed median-green areas on the petals (plate 5, *G–J*).

Spikes were observed in the field with clusters of abnormal flowers surrounded by dwarfed single-lobed bracts (plate 5 *D*) or with 3-lobed, dwarfed leaves arranged to form a rosette, with central, dwarfed, floral parts (plate 5, *E, F;* plate 4, *C*). A considerable amount of variation occurred in the formation of the rosette; often it was composed of 3-lobed leaves, dwarfed sepals, and petals (plate 5, *K*) or cupped leaves and sepals, and dwarfed petals (plate 5, *L*). An examination of the central floral parts of some rosettes under the binocular microscope showed peculiar structures which resembled dwarfed flower buds (plate 4, *E*), sometimes one bud attached by a stalk to another bud (plate 4, *G*), or the carpels replaced by a stem bearing variously modified appendages.

Frequently a proliferation of the apical end of the spike occurred and resulted in variable types of malformations, which confused some grow-

ers, who doubted that all of the extremely varied symptoms were produced by a single virus. Sometimes a dense cluster of leaves enclosed abnormal, green flowers (plate 6, *A*); or a cluster of leafy structures replacing normal sepals, petals, carpels, and stamens, with lower normal-shaped leaves (plate 6, *B*); or linear, leafy structures representing abnormal floral parts with lower single-lobed leaves (plate 6, *C*); or a bunchy, tangled mass of flower parts (plate 6, *D*); or an apical, central cluster of abnormal flowers with filamentous flower organs and lateral branches with dwarfed, apical leaves surrounding abnormal green flowers (plate 7, *A*). The abnormal, green flowers with filamentous sepals and petals were not always found in clusters. They often were arranged and spaced on the spikes like those of healthy plants (plate 7, *B*). Sometimes a cluster of green flowers with long pedicels appeared on the apical end of the spike, with lateral branches surrounded by linear leaves (plate 7, *C*). Numerous slender branches of the spike with dwarfed, abnormal, green flowers suggested a witches'-broom appearance (plate 7, *D*).

Delphiniums naturally infected with aster yellows sometimes show necrotic symptoms on the stems, petioles, and blades, but these symptoms are probably caused by secondary bacterial infections and not directly by the aster-yellows virus. Sometimes such dark-brown or black lesions or necrotic streaks of variable size, shape, diameter, and length occurred on the stems (plate 8, *A, D, E*). Sometimes black blotches girdled the stem (plate 8, *G*) and caused death of the shoots (plate 8, *H*). Sometimes cracks in the stems followed the necrotic streaks (plate 8, *F*). The necrotic streaks appeared on the petioles (plate 8, *A*), sometimes at or near their attachment (plate 8, *C*). Black necrotic specks resembling bacterial leaf spot (plate 8, *C*) occurred on the blades; these often coalesced to form large irregular areas (plate 8, *B*), and sometimes spread over and killed the entire leaf (plate 8, *H*). These symptoms were common on delphiniums grown under natural conditions during the second or later years, but have not been observed on seedlings in seedbeds or cold frames or on experimentally infected plants grown in the greenhouse.

Stalks of delphiniums infected with aster yellows may fall over between the rows before or during the blossoming period. Many of the stalks may be severed but others still adhere to the roots, the leaves often wilting (plate 6, *E*). The stalks frequently showed necrotic streaks and often black lesions. In the spring of 1939 few stalks had dropped up to April 18, but by May 3 it was difficult to walk between the rows owing to the number of stalks which had dropped.

Similar necrotic symptoms on the blades, petioles, and stems, and the lodging or falling over of the shoots have been described by Heald and

Burnett (*6*), Burnett (*2*), and Mulford (*9*) with delphinium "stunt" of Washington, but again these symptoms are probably produced by secondary bacterial invaders and not directly by the aster-yellow virus.

Delphinium seedlings experimentally infected with aster yellows developed greatly elongated, vertical or upright, frequently curved, yellow petioles (plate 1, *B*) with dwarfed, chlorotic leafblades often cupped inward. Naturally infected delphinium seedlings showed similar symptoms except that the petioles were shorter (plate 1, *D*). The greatly elongated petioles developed only when kept in cages in the greenhouse where the light intensity is lower. Delphiniums experimentally infected before or after the spikes began to grow during the second season, developed chlorotic, cupped leaves, often with curved petioles (plate 2, *D*).

The effect of the disease on the flowers was noted on experimentally infected varieties or hybrids. Seedlings infected during the spring often produced a bloom late the first year in the glasshouse, and all infected plants produced abnormal green flowers on the dwarfed spikes. Some of the infected seedlings died before spikes began to grow. Delphiniums infected during the second year before the spikes appeared developed abnormal, green flowers with enlarged, cupped sepals, and sometimes leafy structures from the carpels (plate 3, *C;* plate 4, *F*). Delphiniums infected after the spikes appeared the second year sometimes failed to produce green flowers with abnormal floral parts but developed a dense cluster of short, yellow shoots from the crown after blossoming.

INSECT VECTORS

Three species of leafhoppers have previously been reported (*16*) to transmit the California-aster-yellows virus to aster and celery plants. The short-winged aster leafhopper transmitted the virus with greater efficiency than the mountain leafhopper and the geminate leafhopper. The transmission of the virus by the mountain leafhopper to celery averaged 26.1 and to aster 2.9 per cent, and by the geminate leafhopper to celery 13.7 per cent; but this species failed to transmit the virus to asters. In experiments not previously reported, 120 healthy asters were inoculated, using lots of 3 to 30 male or female geminate leafhoppers to each aster, but not a single case of aster yellows developed, even though a total of 697 adults were used, all of which had completed the nymphal stages on diseased celery plants. During 1941, 25 lots of 50 male geminate leafhoppers reared on diseased celery were transferred to healthy celery plants; and after celery yellows developed, each lot was transferred to 2 successive healthy asters. Typical symptoms of aster yellows appeared on 4 of 50 asters inoculated.

Garden varieties of perennial delphiniums are unfavorable food plants of short-winged and long-winged aster leafhoppers. A high mortality occurred on delphiniums; some of the leafhoppers died within 4 to 6 hours and most of them within 24 hours.

Perennial delphiniums are, however, favorable food and breeding plants of the mountain and geminate leafhoppers under natural conditions. Large populations of nymphs and adults of the mountain leafhopper were taken on perennial delphiniums near Mt. Eden and Capitola during the autumn. Nymphs and adults of the geminate leafhopper were abundant on perennial delphiniums near Salinas. The life histories of both species of leafhopper were completed on delphiniums in the greenhouse.

Vectors Collected on Naturally Infected Delphiniums.—Thirteen lots of 20 male or female mountain leafhoppers collected on delphinium naturally infected with aster yellows near Mt. Eden on October 2, 1937, were transferred to healthy Blackmore and Langdon Giant or Summer Cloud delphiniums, one lot to a plant; 11 of 13 plants, or 84.6 per cent, developed typical symptoms of the disease.

A similar test was made with the geminate leafhopper collected on diseased delphiniums near Salinas on September 15, 1937; 12 of 13 plants, or 92.3 per cent, developed symptoms of aster yellows. Four lots of 20 males, which transmitted the virus to the first set of delphiniums, were transferred to a second set of plants, and all of these became diseased. One lot of 20 males failed to transmit the virus to either of 2 successive delphiniums.

Recovery of Virus from Naturally Infected Delphiniums.—A comparison was made of the ability of the four vectors to recover the virus from naturally infected perennial delphiniums obtained from Mt. Eden and to transfer it to healthy aster or celery plants. The mountain leafhopper and short-winged and long-winged aster leafhoppers were tested by feeding each vector on separate infected delphiniums. In another test, all three of these and also the geminate leafhopper were fed on the same infected plant. Previously noninfective males were used in all tests. The number of delphiniums used in each test, the number of insects on each plant, and the length of time the insects were fed on infected delphiniums, and on healthy aster or celery plants when symptoms failed to develop are indicated in table 1. In spite of the short exposure of delphiniums to the aster leafhopper (6 to 18 hours) high mortality reduced the average number of short-winged aster leafhoppers transferred to aster to 16 per plant and that of the long-winged to 17 per plant even at room temperature. Table 1 shows the recovery and transfer of the virus by the four vectors.

Repeated attempts have been made during the past ten years to recover the virus from naturally infected delphiniums by means of the short-winged aster leafhopper, but all efforts failed owing to the fact that this insect rarely picks up the virus in short feeding periods from diseased delphiniums.

TABLE 1

RECOVERY OF CALIFORNIA-ASTER-YELLOWS VIRUS FROM NATURALLY INFECTED DELPHINIUMS BY FOUR VECTORS

Vector	Length of time fed		Delphiniums naturally infected	Insects on each delphinium	Plants inoculated		Plants infected		Percentage infected
	On delphinium	On aster or celery			Aster	Celery	Aster	Celery	
	days	*days*	*number*	*number*	*number*	*number*	*number*	*number*	*per cent*
Mountain leafhopper (*Thamnotettix montanus*)	7	32	9	20	0	9	..	0	0.0
Short-winged aster leafhopper (*Macrosteles divisus*)	¼–¾	39	25	25–30	25	0	1	..	4.0
Long-winged aster leafhopper (*M. divisus*)	¼–¾	36	19	25–30	19	0	4	..	21.0
Mountain leafhopper (*T. montanus*)*	7	32	24	20	0	24	..	5	20.8
Geminate leafhopper (*T. geminatus*)*	6	34		20	0	24	..	1	4.2
Short-winged aster leafhopper (*M. divisus*)*	¼–¾	39		25–30	24	0	0	..	0.0
Long-winged aster leafhopper (*M. divisus*)*	¼–¾	36		25–30	24	0	4	..	16.7
All vectors			77	.....	92	57	9	6	10.1

* All four vectors were fed in succession on an infected plant and then transferred separately to healthy aster or celery plants.

EXPERIMENTAL INFECTION

Delphinium Varieties and Hybrids.—The following delphinium varieties and hybrids[4] grown from seeds were experimentally infected with the aster-yellows virus by means of four vectors. No attempt has been

[4] Of these delphiniums grown from seeds, nos. 1, 2, and 3 are from Ferry-Morse Seed Co., San Francisco; no. 4 from Germain Seed and Plant Co., Los Angeles; nos. 5, 6, 7, 8, 9, 10, and 11 from Hallawell Seed Co., San Francisco; no. 12 from Aggeler & Musser Seed Co., Los Angeles; and nos. 13 and 14 from Henry A. Dreer, Philadelphia, Pa.

made to determine the species in most cases, since the origin of many garden varieties, hybrids, and races of delphiniums is unknown.

1. Blackmore and Langdon Giants
2. Dwarfed Chinese Blue Butterfly
3. Tall hybrid Bellamosum.
4. Pacific Giant strain
5. Cambridge Blue No. 2828
6. Chinese Azure Blue No. 2821
7. Chinese Dark Blue No. 2822
8. Chinese Blue Butterfly No. 2823
9. Cliveden Beauty No. 2837
10. *Delphinium grandiflorum* var. *album*
11. Improved Wrexham or Hollyhock strain
12. A & M Sunbeam hybrids
13. Dreer's De Luxe hybrids No. 2160
14. White Elatum (Summer Cloud) No. 2149

Incubation Period of the Disease.—The incubation period of the disease was determined in delphinium seedlings and during the second year's growth before and after spikes developed, the later tests being conducted to ascertain the effect of the disease on the flower parts.

Four delphinium varieties or hybrids grown from seeds were inoculated during June. The 12 to 15 plants of each kind were divided among the four vectors, each plant being inoculated singly by one lot of 20 males of one vector. Short-winged and long-winged aster leafhoppers all died within 1 day. The cages containing the mountain or geminate leafhoppers were removed at the end of 1 day from the seedlings and replaced with empty cages. In this experiment all delphinium seedlings inoculated by any of the four vectors developed symptoms of the disease. The length of time from the day of inoculation until the petioles became chlorotic, elongated, vertical, with dwarfed, chlorotic, frequently cupped leaves, was considered as the incubation period of the disease. The results obtained are indicated in table 2. The check, or control, plants of all delphinium varieties and hybrids remained healthy.

The incubation period of the disease was also determined in Blackmore and Langdon Giants and Wrexham delphiniums grown from seeds, kept in a glasshouse during the summer and most of the winter, and inoculated during February, March, and April. To determine the effect of the disease on the flower parts, some of the delphiniums were inoculated before the spike developed and others after the spike began to appear. Each delphinium was exposed to one lot of 20 infective males, one species of leafhoppers being used on each plant. The number of

TABLE 2

INCUBATION PERIOD OF CALIFORNIA ASTER YELLOWS IN DELPHINIUM SEEDLINGS INFECTED DURING JUNE BY FOUR VECTORS*

Variety of delphinium	Plants infected	Incubation period of disease	
		Range	Mean
	number	*days*	*days*
Blackmore and Langdon Giant	12	15–43	27.0
Chinese Azure Blue	12	15–17	16.3
Chinese Dark Blue	15	15–43	17.4
Chinese Blue Butterfly	14	15–43	19.6
All varieties	53	.....	19.5

* Each kind of delphinium was tested with all four vectors (mountain leafhopper, *Thamnotettix montanus;* geminate leafhopper, *T. geminatus;* and short-winged and long-winged aster leafhoppers, *Macrosteles divisus*), each plant being inoculated singly by one lot of 20 males of one vector.

TABLE 3

INCUBATION PERIOD OF CALIFORNIA-ASTER-YELLOWS DISEASE IN DELPHINIUMS* INOCULATED DURING FEBRUARY TO APRIL OF THE SECOND YEAR'S GROWTH

Vector	Plants inoculated	Plants infected	Plants healthy	Incubation period of disease	
				Range	Mean
Delphiniums inoculated before spikes developed					
	number	*number*	*number*	*days*	*days*
Mountain leafhopper (*Thamnotettix montanus*)	6	6	0	29–51	43.7
Geminate leafhopper (*T. geminatus*)	5	5	0	27–81	59.0
Short-winged aster leafhopper (*Macrosteles divisus*)	11	7	4	19–81	45.9
Long-winged aster leafhopper (*M. divisus*)	7	7	0	22–43	30.1
All vectors	29	25	4	.....	43.5
Delphiniums inoculated after spikes developed					
	number	*number*	*number*	*days*	*days*
Mountain leafhopper (*T. montanus*)	5	5	0	29–66	45.8
Geminate leafhopper (*T. geminatus*)	5	4	1	28–44	32.0
Short-winged aster leafhopper (*M. divisus*)	5	0	5	.....	....
Long-winged aster leafhopper (*M. divisus*)	5	5	0	28–106	55.6
All vectors	20	14	6	.....	45.0

* Blackmore and Langdon Giants and Wrexham.

days from the inoculation of the plant until the youngest leaves at the crown of the plant became chlorotic or until green abnormal flower parts developed was considered as the incubation period of the disease; this is shown in table 3. The check plants of both varieties remained healthy.

A comparison of the results obtained in tables 2 and 3 shows that the average incubation periods of the disease in delphinium seedlings infected during June of the first season's growth are shorter than in delphiniums inoculated during February, March, and April during the second year's growth. Temperature and thrifty or vigorous growth probably play important roles in the duration of the incubation period of the disease.

TABLE 4

SUMMARY OF RECOVERY OF CALIFORNIA-ASTER-YELLOWS VIRUS BY EACH VECTOR FROM NATURALLY AND EXPERIMENTALLY INFECTED DELPHINIUMS WHEN TRANSFERRED TO HEALTHY ASTER OR CELERY PLANTS

Vector	Delphiniums tested	Delphiniums from which virus was recovered	Percentage recovery of virus			
			From naturally infected delphiniums (table 1)	From experimentally infected delphiniums	From delphiniums in which incubation period was determined (tables 2, 3)	Weighted mean
	number	*number*	*per cent*	*per cent*	*per cent*	*per cent*
Mountain leafhopper (*Thamnotettix montanus*)	71	13	15.1	18.5	27.3	18.3
Geminate leafhopper (*T. geminatus*)	56	8	4.1	15.0	33.3	14.3
Short-winged aster leafhopper (*Macrosteles divisus*)	104	4	2.2	9.4	0.0	3.8
Long-winged aster leafhopper (*M. divisus*)	94	11	18.6	7.1	11.6	11.7

The infection of delphiniums by four vectors during the second year's growth before spikes appeared was 86.2 per cent and after spikes developed was 70.0 per cent.

Recovery of Virus from Experimentally Infected Delphiniums.—The virus was recovered from experimentally infected delphinium varieties or hybrids, including those plants in which the incubation period of disease was determined. The percentages of recovery of the virus by each vector from naturally and experimentally infected delphinium are shown in table 4, together with the number of recoveries of the virus with each vector and the total number of trials from which the average percentages were computed.

RESERVOIRS OF VIRUS

It is evident that perennial delphiniums serve as reservoirs of the aster-yellows virus. Some commercial growers practice roguing of diseased delphiniums from their fields but pay no attention to the weed reservoirs of the virus. Prickly sow thistle (*Sonchus asper*) growing among delphiniums and along the margin of the fields near Capitola

was commonly found to be naturally infected with aster yellows. Cheeseweed (*Malva parviflora*) was demonstrated to be naturally infected with the disease near Mt. Eden. A large number of weeds have been experimentally infected and many weeds have been demonstrated to be naturally infected with the virus.

CONTROL

Commercial delphinium growers plant seeds in seedbeds or cold frames. An examination of delphinium seedlings grown in seedbeds near Hayward showed the presence of the mountain leafhopper on December 22, 1938, but the geminate leafhopper was not collected; the latter may winter over in the egg stage. Aster yellows and other virus diseases of delphinium were common in cold frames and increased until they were transplanted in the field. Each virus-diseased delphinium transplanted in the field is a source of spread to healthy plants by insects. One grower raised delphinium seedlings in the cold frames under muslin covers to keep out leafhoppers and aphids. Among these seedlings, examined at intervals of 2 weeks until they were transplanted in the field, not a single virus-diseased plant was found.

One commercial grower practiced roguing of diseased delphiniums, and his fields were kept free from weeds, but delphinium aster yellows continued to appear. The mountain leafhopper was extremely abundant in delphinium fields during the summer and autumn in this district.

The weeds on which the four vectors of the aster-yellows virus complete their life histories under greenhouse conditions are being investigated. Field investigations must be undertaken to find the breeding plants of the mountain and geminate leafhoppers and to learn when the flights into the delphinium fields occur, before a spray program can be undertaken. One commercial grower began spraying operations during the spring, but not a single vector of the virus was captured by sweeping delphiniums with an insect net during that season.

The failure of delphiniums grown in home gardens sometimes can be attributed to diseased plants purchased from retail dealers and not always to the spread of the virus by leafhopper vectors after transplanting. All delphinium seedlings grown in flats offered for sale by one dealer in Oakland showed typical symptoms of aster yellows. During the spring of 1937, delphinium seedlings grown in flats were purchased from retail dealers and nurseries in Berkeley and San Pablo and were kept under observation in a glasshouse, but all plants remained healthy. Perennial delphiniums in nurseries in these two localities were usually free from aster yellows. One commercial grower in Berkeley, familiar with some symptoms of aster yellows, rogued the diseased plants.

GEOGRAPHIC RANGE OF VIRUS AND VECTORS

Discussions of host-range differences of California and New York aster yellows, overlapping host ranges, and strains of aster-yellows viruses have been published in previous papers by Kunkel (*8*), Severin (*15*), Severin and Haasis (*24*), and Smith (*26*). The results of experiments with the aster-yellows virus from eastern, middle-western, and western states have also been reported in a previous paper (*15*), and this investigation has been continued on host plants of aster yellows from other western states. The identity of the virus in other western states and the distribution of the most important vectors of the aster-yellows virus to delphinium may be worthy of discussion.

Utah.—Linford (*33, 34*) described typical symptoms of aster yellows on delphinium and also found aster yellows and a "virus-yellows" disease on celery in various localities in Utah.

Severin (*15*) demonstrated that the virus of celery yellows from Utah is probably identical with the California-aster-yellows virus.

Washington.—Heald and Burnett (*6*), mentioned previously, described typical symptoms of delphinium aster yellows occurring in the State of Washington. In a later paper, Burnett (*2*) reported that there was an excessive proliferation of the flowering stalks, which produced a bunchy witches' broom appearance. The flowering parts failed to develop normally but produced a characteristic leafy proliferation varying from slightly greenish flowers to pale-green leafy structures.

Heald[5] has never observed aster yellows in the State of Washington, and he is not convinced that delphinium aster yellows of California is identical with the disease in Washington. He states that juice inoculation from diseased to healthy delphinium plants failed to produce the proliferated inflorescence showing virescence or greening of the flowering parts. But the aster-yellows virus can only be transmitted by leafhopper vectors and by grafting and budding; it is not transmissible by juice inoculation. All attempts at this station to infect healthy Wrexham delphinium, aster, and celery plants grown from seeds by sap inoculation with the carborundum method (*12*) were failures. The inoculated delphiniums were kept under observation until the blossoming period, but none developed abnormal, green flower parts.

Glen A. Huber, Western Washington Experiment Station, Puyallup, Washington, sent 1 delphinium, 3 aster, and 2 celery plants showing typical symptoms of aster yellows. Attempts were made to recover the virus from these naturally infected host plants by means of previously noninfective leafhoppers and to transfer it to healthy seed-grown plants.

[5] Heald, F. D., in a personal interview.

Previously noninfective mountain leafhoppers recovered the virus from the naturally infected delphinium from Washington and transferred it to healthy celery plants. The virus was recovered from the experimentally infected celery plants by means of short-winged aster leafhoppers and transferred to healthy asters. Lots of 20 previously noninfective mountain leafhoppers, after feeding on the experimentally infected celery plants, were transferred to 10 healthy Pacific Giant second-year delphiniums. Three of the 10 inoculated plants developed green, abnormal flowers, numerous short chlorotic shoots grew from the crown of 5 infected delphiniums after the blossoming period, and 2 plants remained healthy. One lot each of previously noninfective short-winged and long-winged aster leafhoppers failed to recover the virus from the naturally infected delphinium and transfer it to healthy delphiniums. The delphinium plant from Washington died before further tests could be made.

Previously noninfective short-winged aster leafhoppers recovered the virus from the 3 naturally infected asters from Washington and transferred it to healthy aster and celery plants and from the experimentally infected celery plants back to asters. Repeated lots of short-winged aster leafhoppers bred on asters experimentally infected with the virus from the 3 naturally infected asters transmitted the virus to 5 Pacific Giant delphiniums; 2 plants developed abnormal flowers with green floral parts, and from the crown of 3 delphiniums grew dense clusters of short, yellow shoots after the flowering period.

The virus was also recovered from the 2 naturally infected celery plants from Washington and transferred to healthy aster and celery plants and from experimentally infected asters back to celery plants. Lots of previously noninfective geminate leafhoppers after feeding on the 2 naturally infected celery plants were transferred to 6 healthy Pacific Giant two-year-old delphiniums; 1 plant showed the green, abnormal inflorescence, and 5 developed numerous chlorotic shoots from the crowns after the blossoming period. The virus from delphinium stunt, and from aster and celery yellows from Washington is probably identical with the California aster-yellows virus.

Colorado.—C. M. Tompkins sent 9 aster-yellows plants from Brighton, Colorado. The virus was transferred from the diseased asters by short-winged and long-winged aster leafhoppers to 9 healthy aster and 3 healthy celery plants. The results indicate that the California-aster-yellows virus occurs in Colorado.

Oregon.—C. M. Tompkins sent 6 aster-yellows plants from Corvallis, Oregon. The virus was transferred by previously noninfective short-winged aster leafhoppers from the diseased asters to 5 healthy aster and

4 healthy celery plants. Thus the California-aster-yellows virus occurs in Oregon.

B. F. Dana, Corvallis, Oregon, sent a delphinium showing phyllody and virescence, but the plant died before any tests could be made.

Wyoming.—At the request of P. Brierly, United States Horticultural Station, Beltsville, Maryland, G. W. Bohn sent aster-yellows plants from Cheyenne, Wyoming. Previously noninfective short-winged and long-winged aster leafhoppers and the mountain leafhopper recovered the virus from 7 diseased asters from Cheyenne and transferred it to 11 healthy aster and 5 healthy celery plants. The virus was recovered from the 3 experimentally infected celery plants and transferred back to asters. These tests indicate that the California-aster-yellows virus also occurs in Wyoming.

Idaho.—At the request of E. C. Blodgett, Idaho Agricultural Experiment Station, C. D. Miller, Mullan, Idaho, sent 2 delphiniums showing witches' broom. Previously noninfective geminate leafhoppers transmitted the virus from the 2 diseased plants to 6 of 11 healthy two-year-old Pacific strain delphiniums but mountain leafhoppers failed to infect 15 delphiniums of the same variety.

Hungerford's (*35*) description of some of the symptoms on delphinium in Idaho are similar to those observed on delphinium naturally and experimentally infected with the aster-yellows virus in California. He states that the aborted flowering parts were very much dwarfed, but he does not mention the green leafy structures representing abnormal flower parts.

There was some variation in symptoms which developed on delphiniums experimentally infected with virus from Idaho. An apical proliferation of the spike developed with numerous 3-lobed green, leafy structures, or single-lobed leaves arranged in a rosette surrounding extremely dwarfed floral organs, or short shoots developed from the spike with linear leaves and an apical leafy cluster surrounding dwarfed flower parts.

Attempts were made to transmit the virus by means of the mountain, geminate, and short-winged and long-winged aster leafhoppers from the 2 naturally infected delphiniums from Idaho and delphiniums experimentally infected with virus from there, to healthy aster, celery, and carrot plants; but all were failures.

Severin (*15*) reported the transfer of an aster-yellows virus by means of previously noninfective short-winged aster leafhoppers from naturally infected carrots sent from Idaho to healthy carrots, but not to healthy aster and celery plants. From a second shipment of naturally infected carrots from Idaho, the virus was transferred to 3 of 61 celery

plants, but the virus was not recovered and transferred to asters from the 3 celery plants showing typical symptoms of yellows.

C. F. Henderson, of the United States Bureau of Entomology and Plant Quarantine, sent a third shipment of diseased carrots from Twin Falls, Idaho. The virus was not transferred from 10 naturally infected carrots by means of previously noninfective short-winged aster leafhoppers to 20 healthy aster and 20 healthy celery plants.

Henderson also sent 12 celery plants from Idaho, each showing a twisting of the central petioles, a symptom of California aster yellows. Previously noninfective short-winged aster leafhoppers failed to transfer the virus from the diseased celery plants to any of 12 healthy celery and 24 healthy aster plants.

The aster-yellows virus in naturally infected delphiniums, carrots, and celery from Idaho, therefore, has not been proved to be the California-aster-yellows virus.

Mountain Leafhopper. — The mountain leafhopper, *Thamnotettix montanus* Van D. has been recorded from British Columbia (*28*), Washington (*31, 32*), Oregon (*32*), California (*29, 32*), Nevada (*3*), Idaho[6], Utah (*7*), Colorado (*4, 28*) and probably occurs in most of the western states.

Geminate Leafhopper. — The geminate leafhopper, *Thamnotettix geminatus* Van D. has been recorded from Colorado (*4, 27*), Idaho (see footnote 6), Utah (*7*), California (*29, 30, 31, 32*), Washington (*11*), and Alaska (*1*). Osborn (*11*) reported that it occurred in such numbers upon clover, alfalfa, and timothy in the State of Washington, especially Pullman, as to threaten to become destructive.

It is evident that one or both of the important vectors of the aster-yellows virus to delphinium in California occur also in Washington, Oregon, Idaho, and Utah, in which states the disease of delphinium resembling aster yellows is known to occur.

Delphinium "stunt" has been reported to occur in New York (*36*), but the mountain leafhopper and the geminate leafhopper do not occur in that state. The short-winged aster leafhopper occurs in New York and it may be possible that the virus of New York aster yellows produces phyllody and virescence in delphinium.

SUMMARY

A virus disease of garden varieties of perennial delphiniums is caused by the virus of California aster yellows. The delay in the discovery of the identity of the virus was caused by the fact that the short-winged

[6] Several shipments of the mountain and geminate leafhoppers were received from Twin Falls, Idaho, collected by C. F. Henderson.

aster leafhopper, *Macrosteles divisus* (Uhl.), rarely recovers the virus from diseased delphiniums. Delphinium is an unfavorable food plant of the short-winged and long-winged aster leafhoppers; some of the leafhoppers died within 4 to 6 hours and most of them within 24 hours.

The main abnormalities resulting from aster yellows on delphiniums may be summarized as follows: (1) dwarfing of plants and a bunchy growth of short stems; (2) a general yellowing of the foliage; (3) phyllody, or the tendency of the floral organs to resemble leafy structures, and (4) virescence, or the replacement of floral pigments by chlorophyll.

The mountain leafhopper, *Thamnotettix montanus* Van D., and the geminate leafhopper, *T. geminatus* Van D., are the most important vectors of the virus to delphinium, and both species breed on this host plant under natural conditions. Adults of both species of leafhoppers were collected on naturally infected delphiniums and transferred to healthy seedlings; the mountain leafhopper transmitted the virus to 84.6 and the geminate leafhopper to 92.3 per cent of the plants. The average percentage of experimental infection of delphiniums by four vectors of the virus was as follows: two-year-old delphiniums before the spikes appeared, 86.2, and after the spikes developed, 70 per cent. The average percentages of the recovery of the virus from naturally and experimentally infected delphiniums by the different vectors were as follows: mountain leafhopper 18.3, geminate leafhopper 14.3, short-winged aster leafhopper 3.8, and long-winged aster leafhopper 11.7.

The incubation periods of the disease in seedlings of four delphinium varieties infected during June by four vectors averaged 19.5 days; in delphiniums infected during the second year in February, March, and April before spikes appeared averaged 43.5; and after spikes developed averaged 45.0 days. Delphiniums infected after the spikes appeared during the second year sometimes failed to produce green flowers with abnormal floral parts, but such plants developed a dense cluster of short, yellow shoots from the crown after the blossoming period.

The geographical range of the California-aster-yellows virus so far determined includes the following states: Oregon, Washington, Utah, Wyoming, and Colorado. The disease of delphinium resembling aster yellows is known to occur in Oregon, Washington, Utah, and Idaho, in which states either the mountain or the geminate leafhopper or both of these important vectors of the virus are known to occur.

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APPENDIX TO CITATIONS

Brief notes of the occurrence of delphinium virus diseases in the United States have appeared in the *Plant Disease Reporter*.[7] Frequently the collaborators of these reports were not mentioned, and it was found more convenient to list them in the chronological order rather than under the name of collaborators and editors.

33. THE PLANT DISEASE REPORTER SUP. 59:111. 1927.
34. THE PLANT DISEASE REPORTER SUP. 65:420. 1927.
35. THE PLANT DISEASE REPORTER 17:5. 1933.
36. THE PLANT DISEASE REPORTER SUP. 90:135. 1935.
37. THE PLANT DISEASE REPORTER SUP. 96:268–69. 1936.
38. THE PLANT DISEASE REPORTER SUP. 110:263. 1938.

[7] A mimeographed pamphlet issued by the United States Department of Agriculture Bureau of Plant Industry.

PLATES

Plate 1.—*A*, One shoot from a dense cluster about 6 inches high showing lateral or axillary shoots with bunched, abnormal leaves, and elongated, chlorotic petioles, also linear or filamentous leaves and threadlike petioles; *B*, Wrexham delphinium seedling experimentally infected with aster yellows showing greatly enlongated, vertical, frequently curved, white petioles with dwarfed, chlorotic leaves; *C*, lower center, normal leaf with 3 lobes or divisions, others, abnormal leaves with lobes partly developed, or 1 or 2 lobes absent; *D*, naturally infected seedling showing symptoms similar to *B* except that the petioles were shorter and most of the leaves were cupped inward. The greatly elongated petioles, such as those in *B*, developed only when kept in cages in the greenhouse.

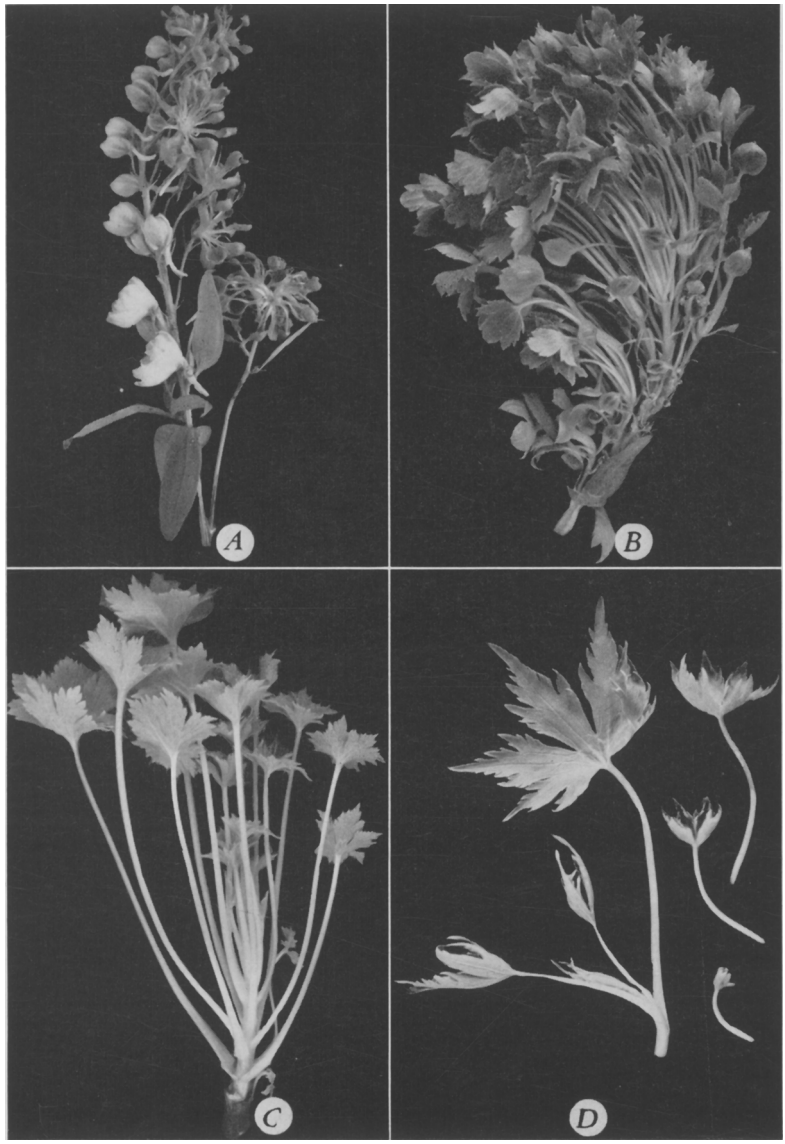

Plate 2.—*A*, Sectorial infection showing normal, colored flowers and abnormal flowers with green, leafy sepals and petals on opposite sides of the spike; *B*, cluster of green, leafy structures replacing normal sepals, petals, carpels, and stamens; *C*, one of many slender shoots which may remain dwarfed until the blossoming period, or may develop a slender spike—the petioles are elongated and yellow, often with chlorotic leaves cupped inward; *D*, chlorotic leaves from a delphinium plant experimentally infected with aster yellows during the second year before spike developed, showing cupped blades and curved petioles.

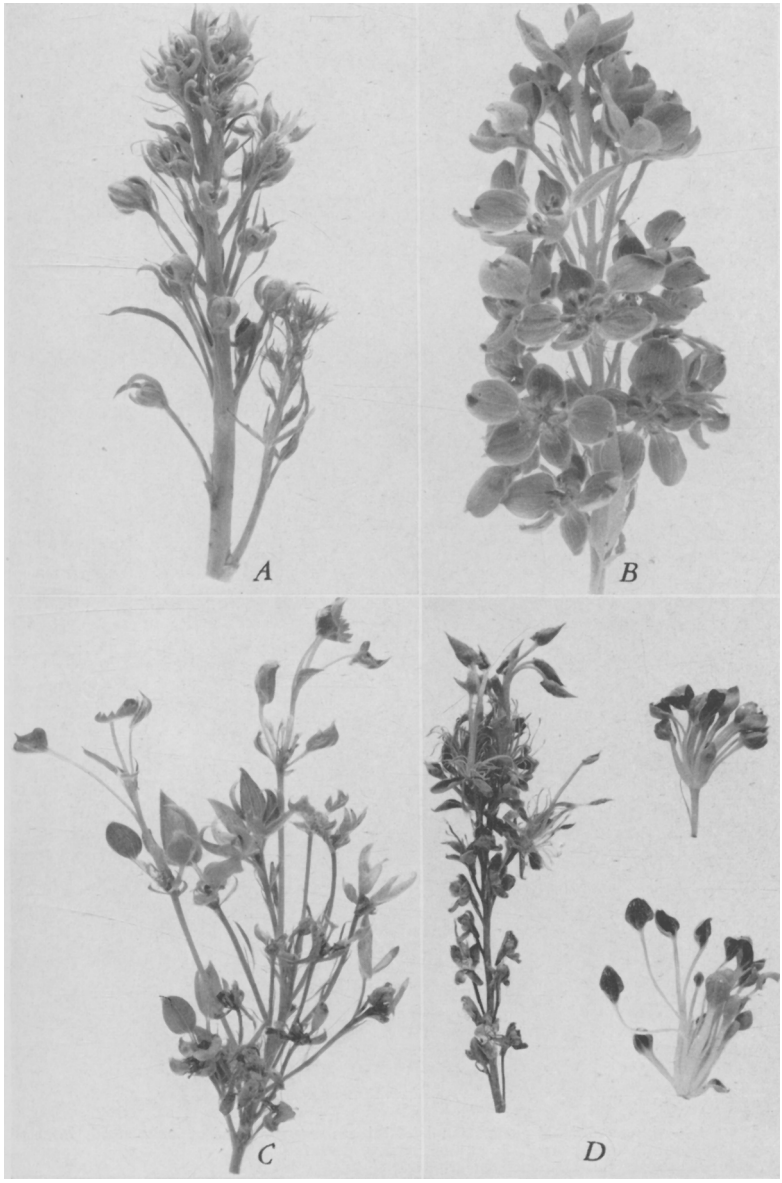

Plate 3.—Apical end of spikes with abnormal flowers from delphinium plants naturally infected with aster yellows: *A*, flower buds which were green; *B*, enlarged green, leafy sepals and dwarfed petals; *C*, replacement of carpels by petiolate leaflike structures or stems; *D*, left, lower flowers which were green instead of blue, upper flowers with elongated stamens and leafy, petiolate, partly opened carpels, which in some cases have lobes resembling ovules; right, two flowers with sepals, petals, carpels, and stamens replaced by green, leafy structures.

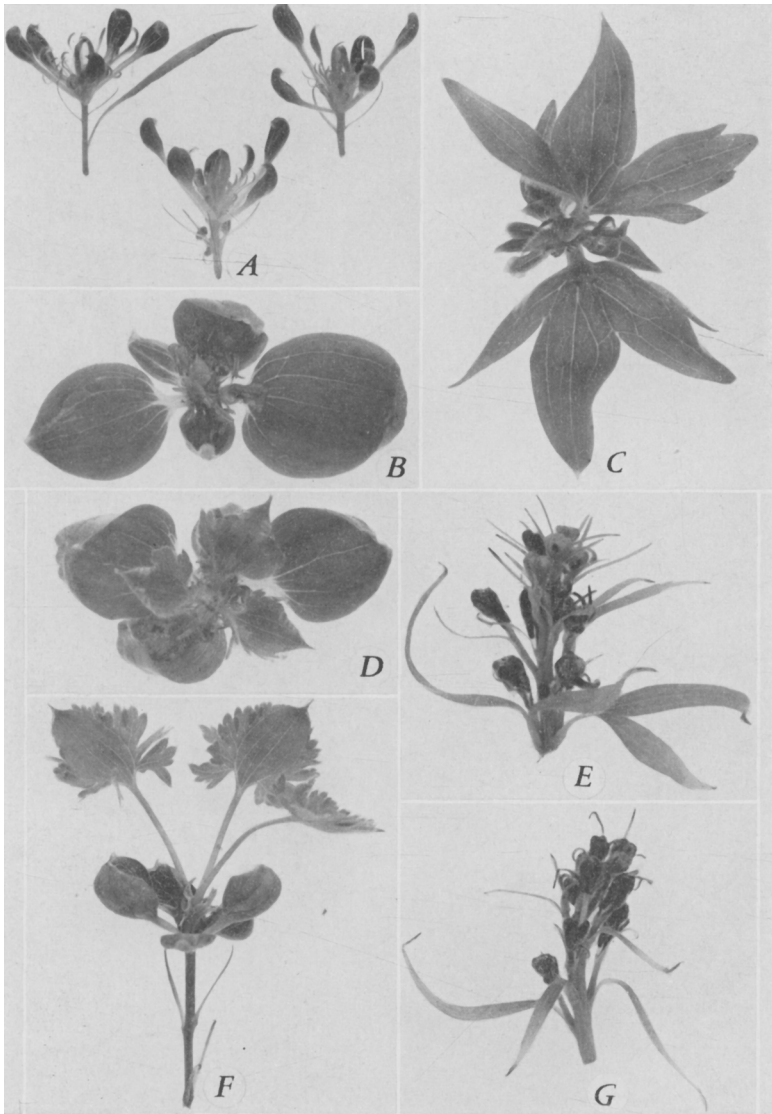

Plate 4.—Abnormal floral parts from delphiniums naturally and experimentally infected with California aster yellows: *A*, cupped sepals, dwarfed petals, and elongated stamens; *B*, enlarged sepals and abnormal floral parts; *C*, 3-lobed leaves and central dwarfed flower parts; *D*, *F*, enlarged, cupped sepals, dwarfed petals, and replacement of carpels by structures resembling leaves; *E*, structures resembling small flower buds; *G*, one stalked bud arising in the center of another bud.

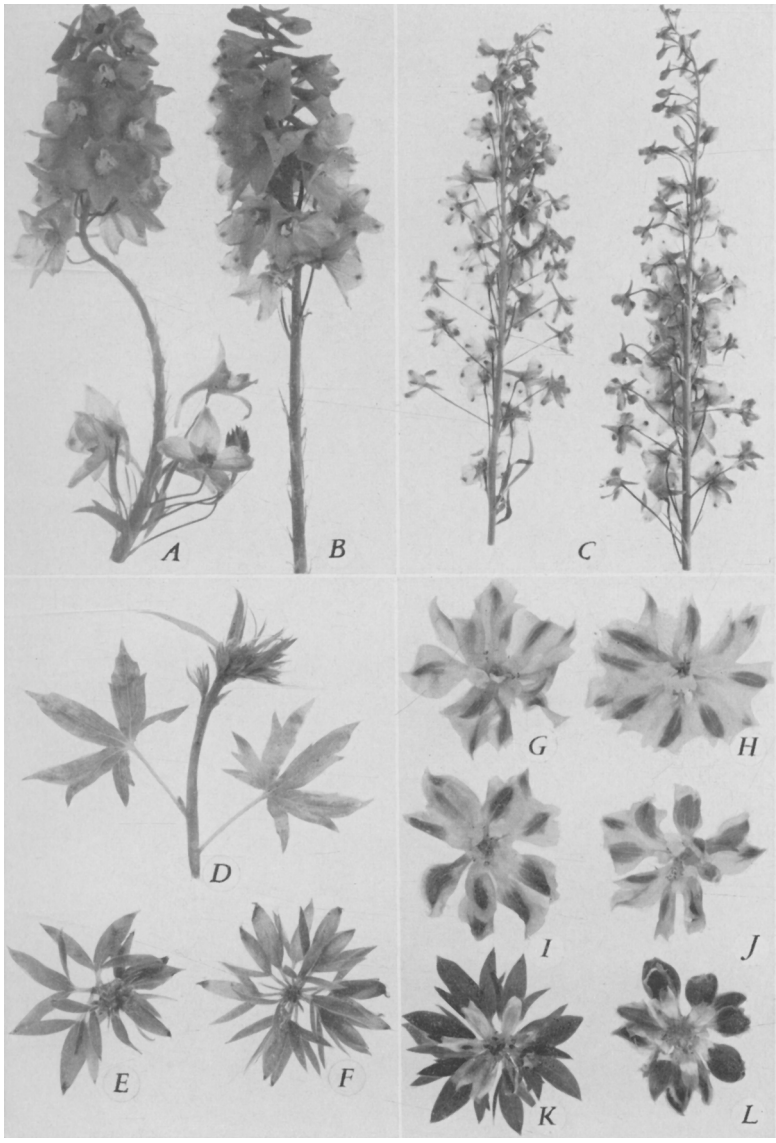

Plate 5.—Abnormal flowers of delphiniums naturally infected with California aster yellows: *A*, cluster of apparently normal flowers on the apical and basal regions of spike with the intermediate part bearing filamentous structures; *B*, cluster of flowers restricted to apical portion of spike; *C*, dwarfed flowers with elongated pedicels; *D*, spike showing apical cluster of abnormal flowers surrounded by dwarfed single-lobed leaves and with lower, normal divisions of leaves; *E*, *F*, rosettes with 3-lobed leaves surrounding undeveloped floral structures; *G–J*, flowers showing median green areas on petals; *K*, rosette composed of 3-lobed leaves, dwarfed sepals, and petals; *L*, rosette with cupped leaves and sepals, and dwarfed petals.

Plate 6.—Proliferation of apical end of spike from delphiniums naturally infected with California aster yellows: *A*, dense cluster of leaves enclosing green flowers; *B*, cluster of leafy structures replacing normal sepals, petals, carpels, and stamens, with lower, normal-shaped leaves; *C*, linear structures representing abnormal floral parts with lower single-lobed leaves; *D*, bunchy, tangled mass of flower parts; *E*, cluster of wilted leaves from fallen stalk still adhering to roots.

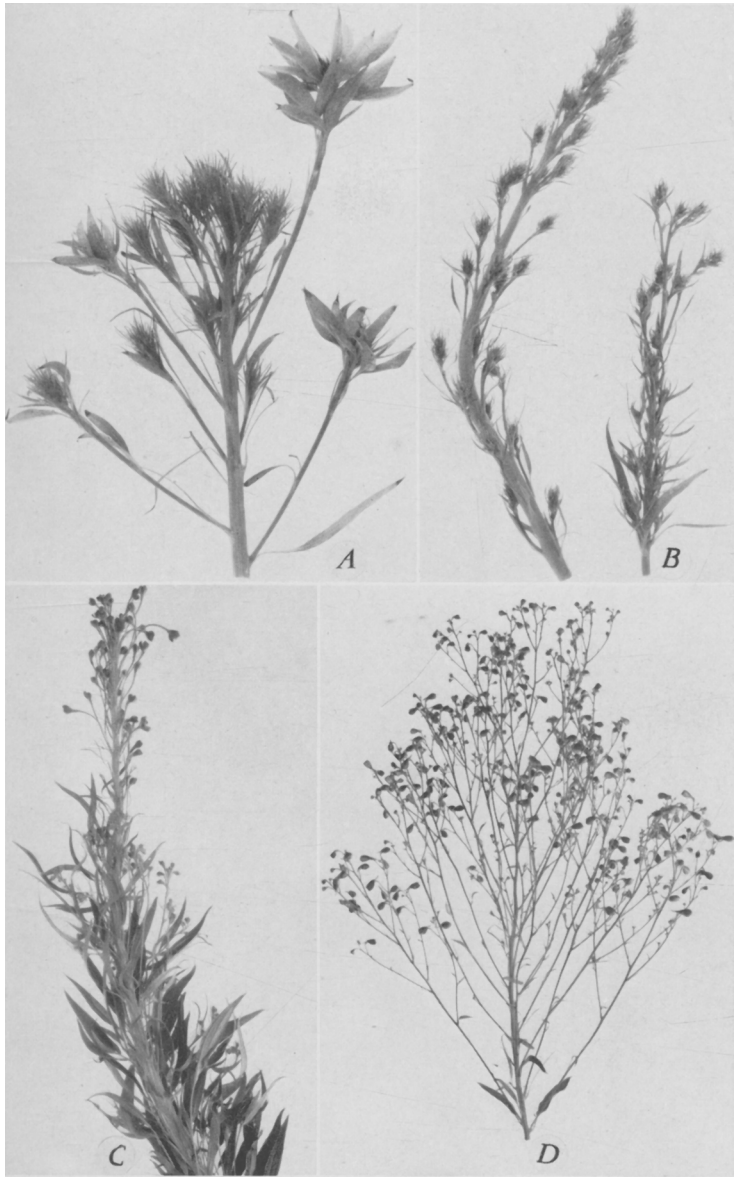

Plate 7.—Apical ends of spikes from delphiniums naturally infected with California aster yellows: *A*, central cluster of abnormal flowers with filamentous flower parts and dwarfed apical leaves surrounding abnormal green flowers; *B*, abnormal, green flowers with filamentous parts arranged and spaced on the spikes like those of healthy plants; *C*, dwarfed, green flowers with long pedicels on apical end of spike with lateral branches surrounded by linear leaves; *D*, numerous slender branches with dwarfed, abnormal, green flowers suggesting a witchs'-broom appearance.

Plate 8.—Dreer's De Luxe delphinium naturally infected with California aster yellows with necrotic symptoms on the stems, petioles, and blades, probably caused by secondary bacterial infections and not directly by the aster-yellows virus: *A*, black, necrotic streaks on stem and on some of the petioles; *B*, black, necrotic tissue on blade; *C*, black, necrotic areas at the attachment of some of the petioles and on some of the blades; *D*, stem showing small, brown, necrotic lesions; *E*, long necrotic streak; *F*, cracks; *G*, black lesions which girdle the stem; *H*, spike showing apical cluster of abnormal flowers, black stem, and dead leaves.