Dispersal of Beet Yellows and Beet Mosaic Viruses in the Inland Valleys of California

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ABSTRACT

Surveys of sugarbeet fields in inland-valley areas of California following intensive spring flights of the green peach aphid indicate that beet mosaic and beet yellows may be markedly reduced by isolating beet fields by 12-15 and 15-20 miles, respectively, from a large area source of infected beets. Early-season mosaic decreased as a parabolic function of distance, whereas early-season yellows decreased linearly with distance from inoculum source. The probable source of infection with both viruses appeared to be infected beets. Phytopathology 60: 798-804.

Three aphid-borne viruses, beet yellows, beet western yellows, and beet mosaic, are extremely common and cause serious losses in root yield of sugarbeets (*Beta vulgaris* L.) in California. They currently pose the most serious threat to successful production of the crop in California.

The present importance of these aphid-borne viruses in the beet crop in the western USA is attributed mainly to the common practice of carrying large acreages of sugarbeets over the winter ("overwintering") and planting new spring crops in the same area. Overwintering plays an important role in distributing the harvest for better use of sugar-processing facilities throughout the year, and has become an economically established practice during the last decade. Unfortunately, this results in the maintenance of a large reservoir of infected plants to provide a source of virus for insect vectors, and has serious implications in the epidemic development of these diseases. Recent efforts at control have aimed at alleviating losses while continuing the economically beneficial practice of overwintering. The present report discusses some of the more important factors in the cyclic development of these aphid-borne virus diseases in California, and presents evidence that isolating fields delays dispersal of two (beet yellows and beet mosaic) of the three aphid-borne viruses involved.

The beet crop itself appears to be the principal, though not exclusive, source of beet mosaic and yellows viruses for introduction into subsequent crops. This was noted first with beet mosaic by Robbins in 1921 (17). He observed that the disease occurred rarely in fields more than 1 mile from infected beets. Pound (15) later noted a similar situation with mosaic. Though he occasionally found the disease to be sporadic in well-isolated fields, no naturally infected nonbeet hosts were found. Watson et al. (26, 27) also observed that, in Europe, mosaic was found only in areas where beet seed crops were carried over the winter.

The situation appears essentially similar with the beet yellows virus. The association solely with beets, however, is less clear-cut, probably because beet yellows virus was confused with the western yellows virus before the latter was described (4, 18). Also, beet yellows

is more widely dispersed by viruliferous aphids than is beet mosaic.

Neither beet mosaic nor beet yellows virus is seed-borne in beets, and although each virus has a potentially wide host range in nature (1, 15), rarely does either infect hosts other than beet. Spinach (*Spinacia oleracea* L.) is the only other cultivated crop in which these viruses may be found in California. In certain localized areas it has been implicated as a source.

The beet western yellows virus differs markedly from mosaic or beet yellows. It has a wide host range, and commonly infects a wide variety of cultivated crops and numerous weed species (6, 19). It is also circulative and persistent in its aphid vector (4, 18), in contrast to beet mosaic virus which is stylet-borne (22, 24). Moreover, though beet yellows virus is retained by aphids for considerably longer periods (24) and exhibits other features in transmissibility dissimilar to the conventional stylet-borne viruses (1), it seems highly probable that it is also stylet-borne in nature. Watson (25) suggested that individual insects lose transmissibility after moulting, though it is not clear whether this was speculation or based on experimental evidence.

Although beet mosaic, beet yellows, and beet western yellows are transmitted by a variety of aphid species, the green peach aphid (*Myzus persicae* Sulzer) is implicated as the most important species in dispersal. The association of the beet yellows virus with migrations of apterous green peach aphid is well established in some parts of Europe (26, 27).

The green peach aphid is the most prominent aphid species associated with beets in both the warm inland valleys and coastal growing areas of the far West (3). Repeated observations indicate that virus spread is closely related to buildup and migration of this species. The association remains largely circumstantial, however, as little evidence exists to the contrary.

The cyclic pattern of aphid buildup and migration has been studied at some length in arid-growing areas of the western USA. It has been established, for example, that reproduction of the green peach aphid in warm inland-valley areas is optimum in the spring, resulting in vast numbers of migrating alatae (3, 11,

14). As the season advances, however, high temperatures curtail reproduction (16), and the species essentially disappears in the warm inland-valley growing areas (2, 3, 11, 12) during the summer. Beets can thus be grown during the summer without infection by the aphid-borne viruses (21), and delayed spring planting may be utilized to escape disease (11). In contrast, the green peach and other aphid species remain active at the moderate temperatures prevailing throughout the growing season in the cool coastal valleys of California.

The limited period of retention (1, 22, 24) and restricted natural host range of the beet mosaic and beet yellows viruses have suggested the use of restricted cropping practices for control, e.g., geographic separation of overwintered and early-spring-planted acreages, plus a crop-free period with the latter (1). These measures seem particularly feasible in the warm inland valleys of California, where the activity of the main vector is largely restricted to the interval before harvest of the overwintered source fields in the spring.

The present investigation obtained data on the distance of dispersal of the two viruses from large sources of infected beets in the inland-valley areas of California. The objective was to evaluate isolation as a barrier to dissemination of the viruses to the early-spring-planted acreage.

MATERIALS AND METHODS.—Beginning in 1964, a number of surveys was made twice yearly for a 5-year period to determine the prevalence of beet mosaic and beet yellows viruses in early-spring plantings of beets at various distances from a large acreage of overwintered fields in the same general area. The surveys covered only early-planted fields (seeded January to March) exposed to major flights of the green peach aphid. The growing area was evaluated in April, when the major aphid flights generally occurred, to determine the proximity of fields to the overwintered acreage and their stage of growth when initially exposed to aphid flights. In some years the surrounding area, particularly that around early-planted fields, was also surveyed for escaped beets, spinach fields, or other possible sources of the viruses. Initial virus surveys were made in late May or early June. These were usually timed about 6 weeks after the major aphid flights, to allow sufficient time for development of symptoms of beet yellows and beet mosaic. Although some secondary spread of the viruses, particularly mosaic, had occurred, the delay was desirable for more exact assessment of beet yellows virus. The early-season surveys were carried out too soon after the major aphid flights for many plants to develop symptoms of beet western yellows virus, which has a longer latent period than beet yellows virus in beets.

Final surveys were made in August (September in 1967) to evaluate final distribution of the viruses before additional spread occurred during the limited fall flights of the green peach aphid. These late-season observations were made in order to increase the sensitivity of the surveys in fields with low levels of infection.

The initial surveys showed that localized growing districts must be chosen carefully to select enough

fields to reflect a gradient of distances from the overwintered acreage while also avoiding large numbers of escaped beets near the early-planted fields being surveyed.

Unlike the situation in Europe (20), we could not reliably distinguish the beet yellows virus from western yellows virus visually. Yellowing of older leaves from beet yellows virus was usually accompanied by discolored or dark necrotic areas, but not always. Vein-clearing characteristic of severe strains of beet yellows, or depressed veins giving an "alligator skin" effect that can be reliably ascribed to infection by the beet yellows virus (1), were found only occasionally. Hence, selected samples from each field were assayed specifically for beet yellows virus by use of an indicator host immune to the western yellows virus (4, 6).

Because of the large acreage of the fields chosen for observation, small portions could not usually be selected for repeated observation that would give a truly representative sample of the whole field. Usually 600-1,200 plants were observed in fields of 20 to 150 acres (8-60 ha). Diseased plants were counted and samples were generally collected from rows 10-20 yards from the field border at six locations distributed around the field. When available, the thickened brittle leaves from the base of plants showing a sectored type of yellowing accompanied by necrosis were collected from more severely yellowed plants for the beet yellows assay.

Assays for beet yellows virus were made by aphid transmission trials to *Chenopodium capitatum* (L.) Asch. Nonviruliferous colonies of green peach aphids were started from newborn nymphs cultured on Chinese cabbage seedlings (*Brassica chinensis* L.) in a refrigerated plastic chamber at about 24 C. Beet leaves were trimmed to fit a petri plate containing discs of moist filter paper adhering to the top and bottom of the dish. Thirty to 40 green peach aphids were placed on each piece of leaf, and the plate was closed, held shut with a rubber band, and incubated at about 24 C for 18-20 hr. The insects were then transferred to healthy seedlings of *C. capitatum* and caged by inverting a plastic drinking glass over the plant for about 24 hr. The plants were then sprayed twice at daily intervals with a solution of nicotine sulfate before being returned to the greenhouse, where they were maintained for 4 weeks and observed periodically for beet yellows symptoms.

RESULTS.—*Spread from areas with large acreages of overwintered beets.*—Most of the surveys were done in a localized region of the Sacramento Valley (Yolo, Solano, and Sacramento counties) adjacent to an intensive beet-growing area in which approximately 30,000 acres are overwintered annually. The overwintered acreage in this area varied from a minimum of 22,600 acres, in 1967, to a maximum of 37,200 acres, in 1964. The amounts of beet mosaic and yellows in fields at various distances from this overwintered acreage are shown in Table 1. Early-spring-planted fields were generally few in the vicinity of this overwintered acreage, for most growers had become aware of the risks. Typical data for a single survey are in Table 2. Decreasing incidence with distance is apparent in the

TABLE 1. Occurrence of beet yellows and mosaic in early-spring-planted sugar beet fields in relation to distance from a large acreage[a] of overwintered fields

Distance from over-wintered fields and disease	% Disease in years designated (fig. in parentheses represent no. fields observed)											
	May-June					5-yr avg	August-September					5-yr avg
	1964	1965	1966	1967	1968		1964	1965	1966[b]	1967	1968	
Less than 2 miles (3.2 km)												
Yellows	11.3(4)	4.0(2)	39.2(3)	91.0(1)	5.3(3)	30.2	24.8(5)	26.5(2)		100 (2)	27.4(3)	44.7
Mosaic	2.0(4)	1.5(2)	26.2(3)	100 (1)	15.7(3)	29.1	17.0(5)	35.0(2)		100 (2)	22.0(3)	43.5
2-5 miles (3-8 km)												
Yellows	23.5(3)	21.8(4)		41.7(3)	14.0(3)	25.3	42.3(3)	56.2(4)		84.5(3)	28.2(3)	52.8
Mosaic	1.0(3)	24.0(4)		68.7(3)	2.6(3)	24.1	5.3(3)	70.1(4)		99.2(3)	11.8(3)	46.6
5-10 miles (8-16 km)												
Yellows	19.7(3)	21.0(3)	26.4(5)	41.5(2)	5.6(1)	22.9	45.6(3)	43.7(3)		80.6(2)	19.6(1)	47.3
Mosaic	2.5(3)	28.0(3)	3.9(5)	66.5(2)	0.1(1)	20.2	14.7(3)	60.3(3)		94.0(2)	5.6(1)	43.7
10-15 miles (16-24 km)												
Yellows	2.9(3)	18.1(1)				10.5	29.8(3)	30.1(1)				29.9
Mosaic	0.2(3)	4.0(1)				2.1	12.8(3)	12.2(1)				12.5
15-25 miles (24-40 km)												
Yellows	0.9(3)	2.5(2)[c]	0.3(3)	0.0(2)	6.7(10)[d]	2.1	17.1(3)	26.0(2)		15.1(2)	26.5(10)[e]	21.2
Mosaic	0.0(3)	0.5(2)	0.0(3)	0.0(2)	0.0(10)	0.1	2.7(3)	3.0(2)		0.0(2)	0.0(10)	1.4

[a] 25,000-35,000 Acres of overwintered sugar beets in the Sacramento Valley.

[b] No late-season surveys made in 1966.

[c] Beet yellows was recovered from only one of these fields in greenhouse assays. Many infected weed beets were found less than 1 mile from this field.

[d] Beet yellows was transmitted from only one plant from each of two fields from a total of 201 plants assayed on *Chenopodium capitatum*.

[e] Beet yellows was recovered from only one plant of 63 assayed from these fields, supporting the contention that much of the yellows observed in late season was due to western yellows.

tables, although this was frequently inconsistent. Variability was great also between individual fields equidistant from the areas with overwintered fields (Tables 1, 2). Thus, in 1965, fields less than 2 miles from the overwintered area had less disease than fields 2-5 miles away, probably because of irregular aphid distribution, though this is speculative. Although high N levels tend to mask symptoms of beet yellows but not of mosaic, in most cases incidence of these two diseases appeared to be strongly correlated. Similarly, the amount of beet yellows virus obtained in bioassays on *Chenopodium capitatum* seemed to be associated with the amount of disease encountered in the field, though too few samples were assayed for quantitative significance.

The relationship between average amount of early season disease and distance for the 5-year period can be expressed as two regression equations that give the best least squares fit to the data (Fig. 1). The amount of beet yellows decreases linearly with distance from inoculum source, whereas the amount of mosaic decreases parabolically with distance. In each case, 98% of the variability in mean disease values is accounted for by the functions described (i.e. for yellows $r^2 = 0.98$; for mosaic $r^2 = 0.98$). The incidence of early disease in each case is about halved 10 miles from the inoculum source. At greater distances, yellows infection continues to fall off at a constant rate (1.51%/mile), whereas mosaic decreases much more rapidly, reaching essentially zero at 13 miles from the inoculum source.

$\hat{Y} = 28.4 - 0.08X - 0.159X^2$ FOR EARLY MOSAIC ($R^2 = 0.98$)

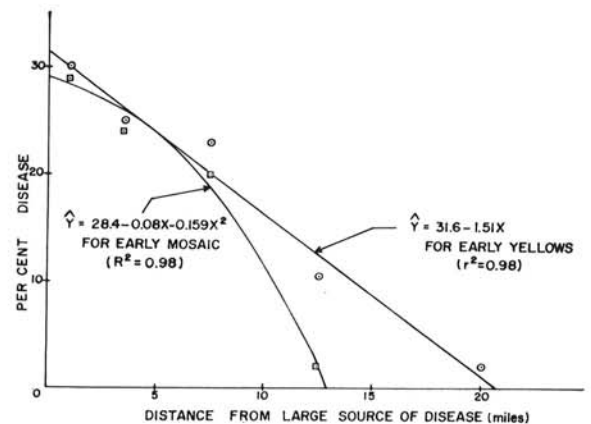$\hat{Y} = 31.6 - 1.51X$ FOR EARLY YELLOWS ($r^2 = 0.98$)

Fig. 1. Distribution of early-season disease of beet yellows and beet mosaic in relation to distance from a large area source (30,000 acres) of infected beets. The amount of disease (Y) at various distances (X) can be expressed by the two regression equations given.

TABLE 2. Incidence of beet mosaic and yellows in early-spring-planted fields in relation to the presence of overwintered fields within a distance of 15 miles in the Sacramento Valley in 1968

Occurrence of over-wintered fields and distance from these	Field counts				Presence of beet yellows in greenhouse assays to Chenopodium capitatum[a]	
	Yellows		Mosaic			
	June	August	June	August	June	August
Overwintering area *miles*						
<2 (3.2 km)	13.2	36.2	11.0	28.3	16/29	
<2	2.6	18.8	26.8	23.8	2/12	
<2	[b]	27.6	9.3	14.5	2/22	
2-5 (3.2-8 km)	21.5	40.3	6.3	18.8	4/29	10/30
2-5	15.5	30.2	0.8	15.3	1/30	2/30
2-5	4.0	14.1	0.6	0.3	0/27	2/30
5-10 (8-16 km)	5.6	16.3	0.2	5.3	1/30	6/30
Without overwintering[c] (no overwintered fields within 15 miles or 24 km)	18.5	40.5	0	0	0/32	0/15
	18.1	36.6	0	0	0/30	
	14.9	41.0	0	0	0/30	0/15
	11.3	22.6	0	0	1/30	0/10
	3.3	18.5	0	0	0/17	0/15
	4.6	34.0	0	0	0/23	0/15
	8.2	32.0	0	0	0/28	
	2.5	14.0	0	0	1/11	1/5
	0.0	16.5	0	0		
	0.7	6.6	0	0	0/4	0/3

[a] The numbers represent the number of plants infected over the total number assayed in each case.

[b] Many plants in this field were chlorotic from N deficiency. It was not possible to distinguish yellows-infected plants accurately in the early-season observations.

[c] This was the 2nd season after overwintering had been discontinued in this area.

Aphid activity for the various years as taken from Hills et al. (11, 12) and Lange et al. (14), is shown in Table 3. The usual prominent peak in activity in the Sacramento Valley area (March, April, and May) extended into June in 2 of the 5 years (1965, 1967). Late-spring flights were associated with late-spring rains accompanied by temperatures cooler than usual. The numbers of migrating alatae encountered were vastly greater in 1 year (1967) than in the other 4 years. Higher levels of infection, particularly noticeable at distances of 5-10 miles, were associated with these unusually high levels of aphid activity, but at distances of 15-25 miles the incidence of disease was not markedly greater with either virus (Table 2).

In some cases, levels of both mosaic and beet yellows were significant near infected weed beets in fields that otherwise had good isolation. Weed beets and "ground-keepers" (small beet roots dropped by mechanical diggers) were frequently encountered in waste areas and in other cultivated crops. In a few cases, several hundred infected beets/acre were observed in culti-vated crops grown in the immediate vicinity of early-spring-planted fields, which probably accounts for mosaic and beet yellows in certain fields relatively far from the overwintered areas.

The late-season surveys showed an increase in both mosaic and yellows (Tables 1, 2), suggesting that spread within the fields after aerial activity by the green peach aphid had ended. The ratio of late-season infection to early infection levels in the 5-year period varied from less than 1 to more than 3 for yellows, and from less than 1 up to 6 for beet mosaic (Tables 1, 2). Individual fields showed much greater increases than these averages (Table 1), being greatest, as expected, in fields with low levels in early season. These increases were unexpectedly great in view of the presumed lack of aphid activity during the summer. The obvious increase in beet yellows was probably largely due to a lack of distinction between beet yellows and western yellows in the late-season observations, when many plants latently infected with western yellows in early season would have been exhibiting symptoms. However, frequent in-

TABLE 3. Aphid flight patterns in the March-June period for 1964-1968 at Davis, California[a]

Year	Approximate mean no. aphids[b] per trap per 2-week periods indicated						
	3/4-3/18	3/18-4/1	4/1-4/15	4/15-4/29	4/29-5/13	5/13-5/27	5/27-6/10
1964			33	56	7	0	0
1965	7	47	32	13	55	10	4
1966	0	68	38	58	4	2	0
1967	3	6	10	33	340	1,700	240
1968	0.9	3.6	46	11	3.0	0.2	0

[a] Data taken from Hills et al. (13), 1965, Lange et al. (14), 1967, and Hills et al. (12), 1967.

[b] Alatae of the green peach aphid—mean no. per 8 yellow pan water traps.

creases in beet yellows recovered from plants taken for bioassays (Table 2) on *C. capitatum* were evident. This suggests that beet yellows spreads significantly in the field after flights of the green peach aphid were no longer detectable.

Results of a survey carried out with early-spring-planted fields in or near the overwintered area and in a similar growing area at some distance from the overwintering area are shown in Table 2. The more distant growing area was maintained as a beet-free area during the winter months for 2 years immediately before the surveys were conducted in 1968. The association of beet mosaic and beet yellows with overwintering beets is shown by these data. No mosaic was observed in the nonoverwintering area, and very little beet yellows was encountered in the bioassays on *Chenopodium capitatum*. The late-season increase in both mosaic and beet yellows was found in fields in which plants were infected in early season, probably representing intra-field dissemination by crawling apterae.

Beet yellows and mosaic in fields near a single over-wintered virus source.—A survey of fields surrounding a single infected overwintered field was conducted in a narrow coastal valley in which fields were distributed both leeward (away from the coast) and windward (toward the coast) from the overwintered field of about 75 acres. The few fields available in each case showed no association of either disease with wind direction. In this survey, beet yellows appeared to be disseminated significantly farther than mosaic (Table 4). The spatial distribution of mosaic was similar to that observed by Duffus (5) in a similar study. Beet yellows, however, appeared to have a significantly greater dissemination than that observed by Duffus. It is perhaps relevant that the cooler summer temperatures in the coastal valleys are conducive to more prolonged aphid activity throughout the growing season, with concomitant "leapfrogging" of disease from one field to another, and rapid and complete dissemination of disease within fields.

Dispersal gradients.—The amount of disease was plotted against distance from the source for comparing the dispersal gradients of beet mosaic and yellows (8, 9). This evaluation used only the data from the experiments dealing with the large overwintering area. For simplicity of computation, the average amount of disease was placed into categories by distance from source (Table 2). To correct for potential multiple infections and to avoid an unrealistic flattening of the gradients at infection percentages over 20%, the amount of disease was converted to potential disease using the multiple-infection transformation (7). The log of the average amount of disease for all fields falling into a particular category by distance was plotted against the log of the distance from source in meters, and the gradients were estimated graphically.

Three of the dispersal gradients (Fig. 2) showed a downward-sloping curvature with increasing distance from disease source, a type commonly encountered with a variety of plant pathogens (8, 23). Except for the curve for late-season yellows, each of the gradients appeared to become steeper as the distance increased. The curves, for example, for early-season yellows and mosaic and late-season mosaic appeared to steepen considerably at 5 to 10 miles from the source (Fig. 2). True gradients for dispersal in these cases would be given by plotting a smooth downward-sloping line through the various points. A line tangent to this curve at any point would be an estimate of the dispersal gradient at that particular distance. For purposes of comparison, however, it seemed most meaningful to divide the curves for early and late-season disease arbitrarily into separate portions by drawing a smooth line through the first several points and another through the last several points.

Evaluation in this manner gave a dispersal gradient for early-season mosaic less than 10 miles from the source similar to that for early-season yellows less than 15 miles from the source, which is itself similar to the entire gradient for late-season yellows. The gradient in each of these three cases is about −0.79. The gradient for late-season yellows was the only one which in its entirety approached a straight line. The gradient for late-season mosaic less than 10 miles from the source is flattened even more markedly (giving a gradient of about −0.344). In contrast, both early- and late-season mosaic farther than 10 miles from the source exhibit very steep gradients of disease. At these distances, the

TABLE 4. Incidence of beet yellows and mosaic in spring-planted fields at various distances from a single overwintered field in a small coastal valley of California[a]

Distance from overwintered field		% Mosaic	% Yellows	Recovery beet yellows to *Chenopodium capitatum*	Presence of escaped or weed beets in vicinity of field[b]	Relative no. escaped or weed beets
Miles	*km*				*miles*	
0.25	0.4	25.0	35.0	+	1/4 (0.4 km)	Many
1.5	2.4	25.0	30.0	+	1/4	Many
1.5	2.4	0.0	2.8	+	1-1/4 (1.6-0.4 km)	Many
4.0	6.4	0.2	0.7	++	1/4	Few
4.3	6.9	0.0	4.0	++	0	
5.8	9.3	0.0	0.75	+	0	
7.3	11.7	0.04	0.13	+	0	
7.3	11.7	0.0	1.8	++	0	

[a] Santa Ynez Valley in Santa Barbara County.
[b] The approximate distance to the nearest source of infected beets other than the overwintered source.
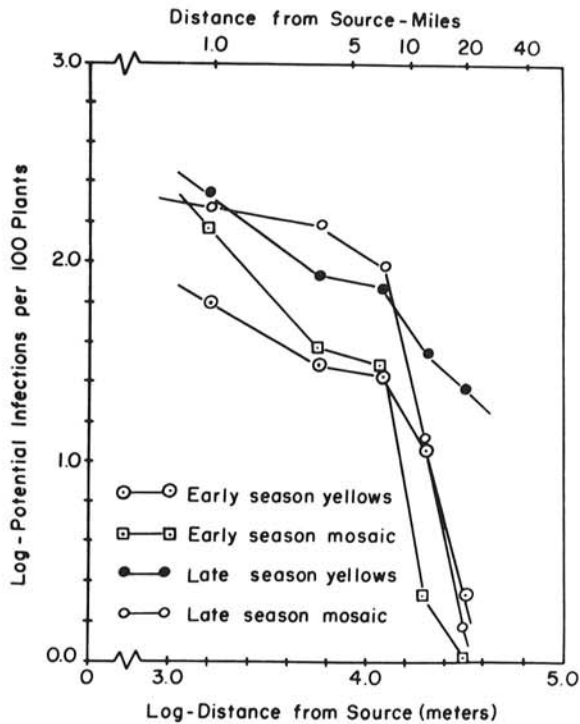
Fig. 2. The dispersal gradients for early- and late-season mosaic and yellows from the large area source of disease.

amount of mosaic varies inversely at a rate in excess of the fourth power of the distance (gradient = -4.33). Early-season yellows exhibited a steep gradient (-2.6) farther than 10 miles from the source, though less than that for mosaic at similar distances from the source.

DISCUSSION.—Many studies have been made of plant disease gradients, and separation of diseased and healthy plants is a familiar way of controlling plant diseases. Control by isolation depends on knowledge of disease incidence with increasing distance from the source, and expected year-to-year variability. Our results indicate that a barrier of 12-15 miles is sufficient for reducing beet mosaic to an insignificant level, and that 15-20 miles would provide an effective barrier to beet yellows virus. In neither case, however, is the distance sufficient to prevent significant dispersal; it merely delays or reduces infection with either virus to a level that is economically trivial.

Use of such isolation by the beet industry in the western desert areas of the USA would require that the industry be organized into discrete planting and harvesting areas. Early-spring-planted acreage intended for fall harvest should be suitably separated from acreage to be overwintered for harvest the following spring. Planting and harvesting within each area should be synchronized to the extent that this is practical, so as to avoid overlapping of crops of successive years within a growing area. Natural geographic barriers between growing areas can be utilized in several cases. The importance of harvesting one crop before planting the next and the need for destroying weed beets has

been stressed by Bennett (1) for increasing the effectiveness of a host-free period.

The relatively flat dispersal gradient for early-season mosaic and beet yellows less than 10 miles from the source is probably due mainly to the vast inoculum in the large area source of disease and the high levels of aphid activity. The flattening of the gradient for mosaic and, to a lesser extent, beet yellows, could have been due partially to secondary spread within fields during the interval between the first aphid activity and the earliest surveys. This would lead to underestimation of the true gradient. Other flattening factors at the shorter distances would be the higher level of background contamination from infected weed beets near the overwintering area and the probability that, at high levels of infection, the multiple-infection transformation would underestimate potential infections. It is known, for example, that the transformation undercorrects at high levels of disease (23). Unfortunately, the early-season results probably do not represent the true primary gradient precisely with either mosaic or yellows because of secondary spread within the fields, and because of background contamination from sources other than the large overwintered source of beets.

The dispersal gradient estimated for late-season yellows deserves special comment, since it probably represents the least reliable of any of the data presented. The disease gradient in this case represents individuals infected with both beet yellows and/or western yellows because of indistinguishable symptoms. Thus, the gradient is essentially one reflecting a great deal of background contamination that markedly flattens the dispersal gradient. Even so, the gradients for early- and late-season yellows have approximately the same slope less than 10-15 miles from the source (Fig. 2).

The dispersal gradients under consideration are probably a composite of several different gradients for the same diseases. For example, during the early-season surveys, infection centers were frequently observed in some fields with both viruses. These usually appear as a conspicuous localized area, several yards in diam, in which all or nearly all plants are diseased. Such infection centers probably represent introduction of the disease by single viruliferous winged aphids, followed by local dissemination by crawling apterae. The dispersal gradient resulting from dissemination by walking insects might be quite different from that produced by aerial activity of the same insect.

The dispersal gradients estimated herein from a large-area source of disease are difficult to relate to the gradients obtained by Gregory & Read (9) for potato leafroll and potato Y viruses from a point source of disease. Both of the latter viruses are aphid-borne, and Gregory & Read's experiments showed gradients of disease varying inversely as the first or second power of the distance around single infector plants placed in potato fields.

Hampton (10), tracing the spread of bean yellow mosaic virus from single perennial red clover fields into snapbeans in the same vicinity, found a conspicuous infection gradient extending for only a few

hundred ft into fields of healthy plants for this stylet-borne virus.

Hull (13) developed a formula for predicting the level of beet yellows in beet fields at various distances from infected beets in Britain that is obviously invalid for the high aphid activity and large acreages of infected plants encountered in California.

The limited dissemination of both viruses during the growing season after cessation of activity by winged migrants of the green peach aphid is probably due principally to crawling aphids within the leaf canopy. In spite of high summer temperatures, low levels of aphid activity probably persist for a considerable period after flights of the insect vector cease, perhaps resulting in considerable dispersal of the disease within individual fields, with little or no inter-field dissemination. Alternatively, significant dissemination by winged migrants of other aphid species could be postulated, but this seems unlikely, since beets can be grown virtually free of the viruses if planted late in the spring in the inland-valley growing areas (12). Similarly, in experimental plantings the viruses introduced into a confined area by aphids in early summer are retained there with little or no dissemination until aerial activity by the vectors resumes in the fall (21).

LITERATURE CITED

1. BENNETT, C. W. 1960. Sugar beet yellows disease in the United States. USDA Tech. Bull. 1218. 63 p.
2. COUDRIET, D. L., & A. M. TUTTLE. 1963. Seasonal flights of insect vectors of several plant viruses in Southern Arizona. J. Econ. Ent. 56:865-868.
3. DICKSON, R. C., & E. F. LAIRD, JR. 1962. Green peach aphid populations on desert sugar beets. J. Econ. Ent. 55:501-504.
4. DUFFUS, J. E. 1960. Radish yellows, a disease of radish, sugar beet and other crops. Phytopathology 50:389-394.
5. DUFFUS, J. E. 1963. Incidence of beet virus diseases in relation to overwintering beet fields. Plant Dis. Reptr. 47:428-431.
6. DUFFUS, J. E. 1964. Host relationships of beet western yellows virus strains. Phytopathology 54:736-738.
7. GREGORY, P. H. 1948. The multiple-infection transformation. Ann. Appl. Biol. 35:412-417.
8. GREGORY, P. H. 1968. Interpreting plant disease dispersal gradients. Annu. Rev. Phytopathol. 6:189-212.
9. GREGORY, P. H., & D. R. READ. 1949. The spatial distribution of insect-borne plant virus diseases. Ann. Appl. Biol. 36:475-482.
10. HAMPTON, R. O. 1967. Natural spread of viruses infectious to beans. Phytopathology 57:476-481.
11. HILLS, F. J., W. H. LANGE, R. L. REED, & R. J. LOOMIS. 1966. Aphid control and planting date for the control of yellows of sugar beet. J. Amer. Soc. Sugar Beet Tech. 14:117-126.
12. HILLS, F. J., W. H. LANGE, & J. KISHIYAMA. 1969. Varietal resistance to yellows, vector control, and planting date as factors in the suppression of yellows and mosaic of sugar beet. Phytopathology 59:1728-1731.
13. HULL, R. 1965. Control of sugar beet yellows. Ann. Appl. Biol. 56:345-347.
14. LANGE, W. H., F. J. HILLS, R. J. LOOMIS, & J. KISHIYAMA. 1967. Early aphid control increases beet production. Calif. Agr. 21:14-15.
15. POUND, G. S. 1947. Beet mosaic in the Pacific Northwest. J. Agr. Res. 75:31-41.
16. REED, J. L. 1964. The influence of certain physical factors on the relative abundance of the green peach aphid, *Myzus persicae* (Sulzer) (Homoptera: Aphididae). Ph.D. Thesis, Univ. Calif., Davis, 151 p.
17. ROBBINS, W. W. 1921. Mosaic disease of sugar beets. Phytopathology 11:349-365.
18. RUSSELL, G. E. 1962. Sugar beet mild yellows virus: a persistent aphid-transmitted virus. Nature (London) 145:1231.
19. RUSSELL, G. E. 1965a. The host range of some English isolates of beet yellowing viruses. Ann. Appl. Biol. 55:245-252.
20. RUSSELL, G. E. 1965b. Observation in the epidemiology of sugar beet virus yellows in Eastern England in 1963 and 1964. Plant Pathol. 14:95-104.
21. SHEPHERD, R. J., F. J. HILLS, & D. H. HALL. 1964. Losses caused by beet mosaic virus in California-grown sugar beets. J. Amer. Soc. Sugar Beet Tech. 13:244-251.
22. SYLVESTER, J. S. 1956. Beet mosaic and beet yellows transmission by the green peach aphid. J. Amer. Soc. Sugar Beet Tech. 9:56-61.
23. VAN DER PLANK, J. E. 1967. Spread of plant pathogens in space and time. Airborne Microbes. 17th Symp. Soc. General Microbiol., London, p. 227-246.
24. WATSON, M. 1946. The transmission of beet mosaic and beet yellows virus by aphids: a comparative study of a non-persistent and a persistent virus having host plants and vectors in common. Roy. Soc. B. Proc. 133:200-219.
25. WATSON, M. A. 1960. The ways in which plant viruses are transmitted by aphids. Rep. 7th Commonwealth Entomol. Conf. p. 157-161.
26. WATSON, M. A., & M. J. R. HEALY. 1953. The spread of beet yellows and beet mosaic viruses in the sugar-beet root crop. II. The effects of aphid numbers on disease incidence. Ann. Appl. Biol. 40:38-59.
27. WATSON, M. A., R. HULL, J. W. BLENCOWE, & B. M. G. HAMLYN. 1951. The spread of beet yellows and beet mosaic viruses in the sugar-beet root crop. I. Field observations on the virus diseases of sugar beet and their vectors *Myzus persicae* Sulz and *Aphis fabae* Koch. Ann. Appl. Biol. 38:743-764.