Beet Western Yellows Luteovirus in Western Oregon

Pathosystem Relationships in a Vegetable–Sugar Beet Seed Production Region

During the 1980s, crisphead lettuce, butterhead lettuce, and spinach crops in western Oregon (Fig. 1) became increasingly damaged by beet western yellows luteovirus (BWYV) (5,8) infection (15), a previously insignificant problem in this area. Utilizing double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) methodology (2), we identified potential BWYV inoculum sources in vicinities of affected lettuce and spinach fields (15) based on the known host range of BWYV (5–9) and prior agroecosystem investigations of BWYV in the Pacific Northwest (20,29,30,32–34,37,38).

In current and prior (14,15) studies, we identified three principal subreservoirs of BWYV inoculum in the Willamette Valley: multiseasonal plantings of vegetable crops, biennial plantings of sugar beet seed fields (21), and numerous BWYV-susceptible weed species prevalent in this agroecosystem (14), including native, introduced, and escaped annual and perennial species. We also endeavored to understand beet western yellows (BWY) disease-cycle components in western Oregon and to document the presence and determine the effects of BWYV in representative western Oregon sugar beet seed fields (17). The incidence of potential aphid vectors on one or more of 30 western Oregon plant species or forms commonly infected by BWYV was also separately examined (16). The purpose of this paper is to present interactions within the BWY pathosystem that cause risks to BWYV-susceptible crops in western Oregon.

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Fig. 1. LandSat-based shaded relief map of the Willamette Valley (complements of Oregon State University Department of Geosciences) showing locations of 10 representative sugar beet seed fields and relative incidence (10 to 90%) of beet western yellows luteovirus (BWYV), 5 May 1992 (Fig. 7). The segment of the Willamette River depicted (black line) extends from Corvallis to Portland. Field locations are oriented by nearest cities. Sugar beet seed field infection by BWYV increased from south to north; in the southern sector from west to east and in the northern sector from east to west. This pattern was largely reproduced during 1993 (Fig. 9). Fresh vegetable production began in the early 1900s in the Columbia River flood basin east of Portland, but processing vegetables now occupy all Valley lowlands included in this map.

History of BWYV-Susceptible Crops in Western Oregon

Vegetable crop production. The fresh market vegetable industry of Oregon first developed in the early 1900s east of Portland. Early vegetable farms were established on either side of a major farm-to-market road near the Columbia River that later became Interstate Highway 30. This early center for fresh-vegetable production lay within 15 miles of the Portland city center. As industrial and residential development displaced vegetable farms after the 1940s, fresh-vegetable production shifted southward to the communities of Gresham and Damascus, and later southward to Canby, Aurora, and Woodburn. Major vegetable-processing plants, first canning, then freezing, were gradually established at vegetable-production localities farther southward in the valley, and by the 1950s, processing vegetables had eclipsed fresh vegetables in western Oregon. A few farms east of Portland continue to produce fresh vegetables for local markets.

Sugar beet seed production. The West Coast Beet Seed Company, established near Salem, Oregon, in 1940 (21), was the first beet seed company in the United States. Western Oregon was chosen by leaders in the sugar beet industry for its cool, mild winters that provided "photo-thermal induction" of fall-planted beet plants (i.e., that optimized seed production

in the following year) and minimal freeze damage to overwintering roots. This seed company was founded by sugar company leaders and became the exclusive supplier of sugar beet seed to all major U.S. sugar companies. The company also worked with breeders in continuous efforts to improve sugar beet varieties, including seed increases of sugar beet breeder progenies and genetic stocks. Average annual sugar beet seed production in the Willamette Valley has typically exceeded 10 million pounds, and all U.S. beet sugar production is dependent on this seed-production region.

History and Traits of BWYV

BWYV in the United States and the World. Duffus (5) initially differentiated BWYV from beet yellows closterovirus in 1960, based on host range and later on distinct serological and biological properties (6,8,9). Wallis (37,38) identified several weed hosts of BWYV and found that the green peach aphid (*Myzus persicae* (Sulzer)) was a principal vector of BWYV in the Pacific Northwest. Soon thereafter, Howell and Mink (20), Tamaki (30), Tamaki et al. (32), and Tamaki and Fox (29) further elaborated the natural spread of BWYV by *M. persicae* (30) relative to BWYV incidence. Thomas (33) described the dissemination of BWYV in eastern Washington, and Howell and Mink (20) implicated volunteer sugar beet plants as an important BWYV inoculum source in that region. During this period, BWYV was also detected in vegetable and weed species in Illinois (35), as well as in other parts of the world, including Japan (27), Europe (9), Israel (26), and Australia (22).

Symptoms induced by BWYV. Induction of chlorotic (yellows) symptoms, the trait for which luteoviral diseases were named, is well illustrated in BWYV-infected head lettuce (Fig. 2). Typically, symptoms are first observable at the tips or margins of leaves and soon involve whole leaves. Interveneal chlorosis (leaf veins remaining green) first occurs in older

leaves and progresses acropetally, followed by necrosis. However, rapid collapse of infected tissues, necrosis, and severe stunting are not uncommon among BWYV hosts. With the impairment or loss of chlorophyll, anthocyanin accumulates in the leaves of some BWYV-infected plant species (Figs. 3 to 5), resulting in reddish veins, blotches, or reddish patterns similar to the chlorosis induced in other species. BWYV-induced symptoms in peas are identical to those produced by bean leaf roll luteovirus (13).

Certain herbicides, including endothal and pronamide, can induce red-leaf symptoms in some weed species that are identical to those caused by BWYV infection (Fig. 5A). BWY symptoms may also approximate those caused by nutrient deficiencies. For instance, the interveinal chlorosis of older lettuce leaves closely resembles magnesium deficiency, whereas symptoms in younger leaves of many plant species resemble iron-deficiency symptoms. Tip bronzing and necrotic spots on leaves of BWYV-infected pigweed plants (Fig. 3A) may closely mimic potassium deficiency symptoms.

Epidemiological properties of BWYV. BWYV is neither mechanically transmissible nor seed transmissible but is spread in nature exclusively by several aphid species (1,5) in a persistent (circulative), non-propagative manner (8,39). BWYV is exceptional among luteoviruses in having a very wide host range that includes more than 100 species in at least 21 dicotyledonous plant families (8). It is likely that other hosts of this virus remain unknown. Four seemingly unreported hosts of BWYV (Table 1) were identified by Hampton et al. (14; Table 1).

BWYV in northwestern North America. The presence and spread of BWYV in the Pacific Northwest were first documented by Wallis (37,38) soon after the virus was first described (5). BWY epidemics in western Oregon vegetable crops became progressively more severe during the 1980s (15), a period during which re-

Fig. 2. Typical luteovirus symptoms in a field of head lettuce located northeast of Woodburn, showing two levels of tolerance to beet western yellows luteovirus (BWYV) infection (A). Note yellows-affected lettuce leaf (B) with characteristic marginal and interveinal chlorosis. An earlier infected head, left, was severely stunted; leaves that had been chlorotic later became necrotic. BWYV-infected lettuce heads are unmarketable, as are infected spinach plants; therefore, incidence of infected plants equals crop loss.

Fig. 3. Beet western yellows luteovirus (BWYV)-induced chlorosis, bronzing, and necrotic spots in leaves of pigweed (*Amaranthus powellii*) (A), symptoms that could be confused with those caused by nutritional deficiencies. Yellow and red pigmentation in leaves of BWYV-infected spinach plants, emphasized by backlighting (B).

search on BWYV was expanded in British Columbia (10–12). British Columbia crops reported to be infected with BWYV (24) were identical to those later found to be infected in western Oregon. While investigating the reported role of BWYV as a potato pathogen, Ellis (10,11) tested large numbers of many weed species as possible alternate hosts of BWYV. Comparisons of our data with those of Ellis indicated that the inoculum reservoir of BWYV in weed species was more restricted in British Columbia than in western Oregon (14), both in the number of weed species infected and in the incidence within species.

Although the timing of BWYV entry into western Oregon is uncertain, the event probably occurred many decades ago by migratory flights of viruliferous aphids. In 1940, when sugar beet seed production began in western Oregon (21), no prior-season roots ("stecklings") were involved in sugar beet seed production, thus mini-

mizing BWYV introduction into the region in infected sugar beet roots. At least six aphid species recognized as BWYV vectors and known to occur in western Oregon (16) could have been instrumental in its establishment and dissemination among crop and weed hosts. These include: *Aphis gossypii* Glover, *Aulacorthum solani* (Kaltenbach), *Brachycaudus helichrysi* (Kaltenbach), *Brevicoryne brassicae* (L.), *Macrosiphum euphorbiae* (Thomas), and *Myzus persicae* (Sulzer). The mild winters of the Willamette Valley assure the survival of BWYV in infected crops, weed species, and aphid vectors.

Vegetable crops susceptible to BWYV have thus been grown commercially in western Oregon for more than eight decades, and sugar beet seed crops have been grown interspersed among these vegetable crops for more than five decades. Both kinds of crops have long coexisted with weed species susceptible to BWYV. More-

over, these three subreservoirs of BWYV exist within a climate and agroecosystem enabling aphid-vector populations to overwinter and thrive.

BWYV Assays

ELISA systems and preliminary incidence assessment of BWYV. Polyclonal luteovirus antisera and monoclonal antibodies were tested against extracts of healthy plants (negative controls) and plants infected with BWYV type isolates (positive controls). Polyclonal luteovirus antisera kindly provided by P. E. Thomas (33,34) were evaluated individually for BWYV specificity, detection sensitivity, precision, and simplicity, as were monoclonal antibodies kindly provided by C. D'Arcy (4) and P. Ellis (10,12). Most of the data reported herein were obtained by use of the P. E. Thomas BWYV-specific polyclonal antiserum and the DAS-ELISA

Fig. 4. Beet western yellows luteovirus (BWYV)-induced symptoms in plants of field mustard (*Brassica campestris*) (A) and dog fennel (*Anthemis cotula*) (B). Reddish pigmentation on the lower leaves of mustard plants was closely associated with detection of BWYV by double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA). Progressive emergence of mustard seedlings (note small plants, lower right) and other BWYV-susceptible weed species provides year-round carryover of BWYV inoculum in western Oregon. The dog fennel plant on the right was asymptomatic and was free of ELISA-detectable BWYV. The other three plants were BWYV infected and illustrate a gradient (R to L) of BWYV-induced leaf reduction and reddening.

Fig. 5. Red stem filaree (*Erodium cicutarium*) (A) and subterranean clover (*Trifolium subterraneum*) (B) are not only susceptible to beet western yellows luteovirus (BWYV), but their low-lying leaves provide protection and overwintering sites for several aphid species, including *Aulacorthum solani* and *Myzus ornatus*, both recognized vectors of BWYV. The red stem filaree plants illustrate a gradient of increasing BWYV-induced red and yellow foliage and stunting, clockwise from upper left. All four plants contained enzyme-linked immunosorbent assay (ELISA)-detectable BWYV. The healthy subterranean clover plant, upper left, contrasts with the lower four plants, all infected with BWYV. The necrotic plant, upper center, was infected by both BWYV and root rotting fungi. The diseased plant, upper right, was infected by pea enation mosaic virus (a recognized virus-plant association in the Willamette Valley) but contained no ELISA-detectable BWYV.

two-step method (23). Otherwise, reagents and protocols corresponded to those prescribed by Converse and Martin (2).

Plant samples were labeled by date, location, plant species and variety where needed, and presence or absence of luteovirus-like symptoms. Tissue extracts from each sample were tested in at least two microtiter plate wells. Tissue extracts from BWYV-infected turnip plants and from healthy sugar beet or pea plants were included in each microtiter plate.

Because we chose to emphasize crop-weed associations, most weed samples were gathered either within fields of crops found to be BWYV-infected or from border areas of such crop fields. Variability in populations of weed species among these sites precluded uniform representation of weed species tested for BWYV infection (Table 1).

Preliminary assays in 1986 and 1987 indicated that BWYV was detectable in 5 to 7% of pea and broccoli crop plants, 5 to 15% of sugar beet seed plants, and 25 to 30% of field mustard (weed) plants.

BWYV in vegetable crops and associated weeds. Incidence of BWYV-infected plants in 30 crop and weed species tested

Fig. 6. Sugar beet seed fields that contain abundant weedy hosts of beet western yellows luteovirus (BWYV) are typically infected with BWYV at higher rates than are weed-free plantings. The wild radish plants (*Raphanus sativa*) (A) in this field escaped fall-applied herbicide, providing BWYV inoculum for at least 6 months, for aphid transmission to sugar beet plants. A more abundant inoculum supply was provided by field mustard (*Brassica campestris*) in another sugar beet seed field (B). Such plants, when assayed for BWYV in January and February, usually contained a higher virus incidence than did the associated sugar beet plants, indicating that field mustard was an early spring source of BWYV inoculum for spread by aphids.

Table 1. Crop and weed species in the Willamette Valley of western Oregon in which beet western yellows luteovirus (BWYV) was detected by double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA)

Binomial	Common name	No. plants detected/tested	
		Symptomatic	Asymptomatic
Northern valley			
<i>Amaranthus blitoides</i> Wats.	<u>Prostrate amaranth</u> ^a		4/7
<i>Anthemis cotula</i> L.	Dog fennel	2/4,1/1,5/5 (R) ^{b,c}	1/5
<i>Beta vulgaris</i> L.	Sugar beet (seed)	3/8 (Y)	10/30
<i>Beta vulgaris</i>	Garden beet	8/20,6/6 (S)	
<i>Beta vulgaris</i> subsp. <i>cicla</i> L.	Swiss chard	4/5(S)	
<i>Brassica campestris</i> L.	Field mustard	5/5,6/6 (R)	3/10,8/53
<i>Brassica nigra</i> (L.) Koch	Black mustard		0/2,1/1,1/1,1/2
<i>Brassica rapa</i> L.	Turnip	3/3 (Y)	
<i>Capsella bursa-pastoris</i> (L.) Medik.	Shepherd's-purse ^d	0/10,0/6 (Y)	
<i>Cirsium arvense</i> (L.) Scop.	Canada thistle		4/5,3/10
<i>Geranium dissectum</i> L.	Cut leaf geranium	1/1 (R)	0/2
<i>Lactuca sativa</i> L.	Lettuce (grower)	10/12,4/4 (Y)	0/6
<i>Lactuca serriola</i> L.	Prickly lettuce ^e		0/6,10/10,0/11,0/5
<i>Raphanus sativus</i> L.	Wild radish		8/20
<i>Senecio vulgaris</i> L.	Groundsel ^e		1/10,0/1
<i>Spinacia oleracea</i> L.	Spinach (grower)	26/30 (Y/R)	3/14
<i>Stellaria media</i> (L.) Vill.	Chickweed ^f		0/7,0/20,0/2
<i>Trifolium pratense</i> L.	Red clover	5/6,2/3 (S)	3/3
<i>Trifolium subterraneum</i> L.	Subterranean clover	4/4,2/3 (S)	1/1
Southern valley			
<i>Amaranthus blitoides</i>	<u>Prostrate amaranth</u>	1/1 (Y)	
<i>Amaranthus powellii</i> Wats.	Pigweed	8/11,5/5 (Y)	
<i>Anthemis cotula</i>	Dog fennel	3/3,4/4 (R)	0/2
<i>Archium minus</i> Benth.	<u>Burdock</u>		2/6,3/6
<i>Beta vulgaris</i>	Sugar beet (prelim.)	(1987) 3/20 (Y)	(1986) 1/20
<i>Beta vulgaris</i>	Garden beet	11/15,12/15 (Y/R)	0/3,3/7
<i>Brassica campestris</i>	Field mustard	4/4 (R)	2/6,2/2,10/58
<i>Brassica oleracea</i> var. <i>italica</i> Plenck.	Broccoli	8/10,5/5 (Y)	3/5
<i>Brassica rapa</i>	Turnip	6/15 (Y)	
<i>Capsella bursa-pastoris</i>	Shepherd's-purse	0/5, 1/5 (Y)	
<i>Cirsium arvense</i>	Canada thistle ^e		0/4,3/6,0/7
<i>Crepis setosa</i> Hallier. f.	<u>Bristly hawkbeard</u>		4/10
<i>Erodium cicutarium</i> L'Her.	Red stem filaree	6/6 (R)	0/1
<i>Geranium dissectum</i>	Cut leaf geranium	1/1 (R)	0/2
<i>Lactuca sativa</i>	Lettuce (plots) ^g	4/5,8/12,2/2 (Y)	
<i>Phaseolus acutifolius</i> var. <i>latifolius</i> Freem.	<u>Tepary bean</u> (plots)	3/5 (Y)	
<i>Pisum sativum</i> L.	Garden pea (plots)	10/13,12/18,8/8 (Y)	0/2
<i>Raphanus sativus</i>	Wild radish	2/8,3/10,1/2 (Y)	
<i>Senecio vulgaris</i>	Groundsel	9/9 (R)	0/2
<i>Sonchus oleraceus</i> L.	Common sowthistle	1/1 (Y)	1/1,0/1
<i>Spinacia oleracea</i>	Spinach (plots)	4/5 (S)	0/3
<i>Stellaria media</i>	Chickweed ^e		0/31,1/10,1/10
<i>Tetragonia expansa</i> Murr.	New Zealand spinach (plots)	2/3,1/1,1/1 (S)	1/3
<i>Trifolium subterraneum</i>	Subterranean clover	4/4,2/3 (S)	
<i>Vicia faba</i> L.	Faba bean (plots)	4/4,2/3 (Y)	2/10
<i>Vicia sativa</i> L.	<u>Common vetch</u> (weedy)	1/1 (R)	0/4

^a Common names underlined appear not to have been reported as hosts of BWYV before 1991.

^b Data separated by commas indicate separate locations of collection.

^c BWYV-induced symptoms: (S) = symptom complex typically including plant stunting, leaf and stem distortion, yellow or red leaf and stem pigment development, or tissue necrosis (Fig. 5); (Y) = leaf margin and interveinal chlorosis, beginning with older leaves (Fig. 2B); and (R) = red leaf pigment development, beginning with older leaves (Fig. 4).

^d Plants of *Capsella bursa-pastoris* were collected specifically for symptoms typical of those induced by BWYV in this species. Failure to detect BWYV in such plants suggested the possibility of infection by a distinct luteovirus(es).

^e Incidence of BWYV in weed species varied markedly among locations, e.g., *Lactuca serriola* and *Senecio vulgaris*, northern valley, and *Cirsium arvense* and *Stellaria media*, southern valley.

^f *Stellaria media*, a known host of BWYV (5), was a common weed in severely beet western yellows-affected northern valley lettuce fields; however, the sampled plants neither exhibited luteovirus-like symptoms nor contained ELISA-detectable BWYV.

^g Plots: These six crop species so noted were available for sampling in the southern valley only in experimental plots.

during 1988 to 1991 (14,15) is presented in Table 1. Twenty-two per cent of all asymptomatic weed and crop plants contained ELISA-detectable BWYV (101/456), whereas 69% (261/380) of those with luteovirus-like symptoms contained detectable BWYV. Weeds whose common names are underlined were not reported as BWYV hosts before 1991 (14). Luteovirus-like symptoms were good indicators of BWYV infection in some crop and weed species, including lettuce, spinach, garden beet, dog fennel, field mustard, red stem filaree, and groundsel. The most often encountered

BWYV-susceptible weeds in Willamette Valley vegetable and sugar beet seed fields were pigweed (Fig. 3A), field mustard (Fig. 4A), wild radish (Fig. 6A), and dog fennel (Fig. 4B). Chickweed and shepherd's-purse were also very widespread in some lettuce and spinach fields, but BWYV rarely occurred in either species, even when the latter expressed luteovirus-like symptoms. Both are generally infected with BWYV in central California (7).

No ELISA-detectable BWYV occurred in the following crop or weed species (reported BWYV hosts underlined; number

of plants tested in parentheses): *Brassica caulorapa* (6), *Cardamine oligosperma* (10), *Cerastium vulgatum* (11), *Convolvulus arvensis* (12), *Daucus carota* (21), *Echinocystis oregana* (2), *Epilobium angustifolium* (4), *Euphorbia lathyris* (2), *Hypochaeris radicata* (6), *Matricaria matricaroides* (10), *Plantago major* (6), *Polygonum aviculare* (3), *Portulaca oleraceae* (5), *Radicula armoracia* (10), *Senecio jacobaeae* (10), *Sisymbrium officinale* (9), *Solanum nigrum* (7), *Sonchus arvensis* (6), *Sonchus asper* (6), *Taraxacum officinale* (6), *Trifolium repens* (2), and *Veronica persica* (8). As with other weed species, these were sampled principally at locations where associated crops had become infected with BWYV. Failure to detect BWYV in these species could have been due to small numbers of plants available for testing, to their having escaped vector inoculation, to limitations of host-specific vectors, or to inherent plant biotype immunity to BWYV.

BWYV incidence in sugar beet seed crops and associated weeds. Cooperative investigations with West Coast Beet Seed Company, Salem, began in 1992 to assess BWYV incidence in sugar beet seed fields selected to represent the historic distribution of this crop in western Oregon. In a single crop, under this industry umbrella, we were able to visualize BWYV distribution over an 80 × 40 km area of the Willamette Valley. Ten sugar beet seed fields were selected within this area, sampled, and tested for BWYV incidence at four dates in 1992, before July seed harvest (Figs. 1 and 7). A 60 × 30 m sampling area was selected for each field, within which an oval sampling pattern was repeated on each sampling date. Median-age leaves were sampled from 10 or 20 plants from each field, and the order of sampled leaves was preserved for laboratory processing. Sampling the same plants was avoided in

Fig. 7. Incidence of beet western yellows luteovirus (BWYV) in 10 selected sugar beet seed fields sampled on four dates during 1992. Zero levels of enzyme-linked immunosorbent assay (ELISA)-detectable BWYV on one or more sampling dates in fields 1, 51, 60, 70, and 39 were given values of 2%, for graph visibility. Fields 70, 102, and 33, in the northwest sector of the test area (Fig. 1), were infected with BWYV at the highest rates. Fields 1, 51, and 39, in the south-southwest perimeter area, were infected at the lowest rates.

Fig. 9. Sugar beet seed fields, located near six of the 10 fields tested in 1992 (Fig. 8), were sampled on 8 June 1993 and tested for beet western yellows luteovirus (BWYV) incidence. Low BWYV incidence in the 1992 south-southwest perimeter (fields 51 and 39) and high virus-incidence in the northwestern sector (field 102) recurred in 1993. The field 60 locality remained intermediate in BWYV-incidence in 1993. The field 11 locality, registering the highest BWYV incidence of 10 fields in January 1992, had a June 1993 BWYV incidence of 87%, equal to that of field 102.

Fig. 8. Most sugar beet seed growers in western Oregon achieve excellent weed control and thereby minimize in-field beet western yellows luteovirus (BWYV) inoculum sources. This field, weed-free before a February foliar application of nitrogen (urea) fertilizer, with pronamide and endothall herbicides, remained free of weedy BWYV sources until the July seed harvest. These plants had recovered from chemically induced leaf injury within a few days, grew luxuriantly, and yielded high-germ, high-vigor seeds.

subsequent collections to minimize mechanical or physiological effects on sampled plants, to increase the total number of plants sampled, and to test the congruity of BWYV-incidence data among sampling dates. Some of the 10 selected fields were essentially free of weeds (Fig. 8).

No BWYV was detected in four of the fields in January (fields 1, 51, 60, and 70) (Fig. 7). However, all fields contained ELISA-detectable BWYV in February, and BWYV typically reached maximal incidence in April or May samples. The high May incidence of BWYV in fields 70, 102, and 33 tentatively defined a core of high BWYV incidence with a roughly south-to-north gradient of increasing incidence (Figs. 1 and 7), a pattern largely reproduced in 1993 (Fig. 9). Although sugar beet seed crops are never consecutively planted in the same field, sugar beet seed plantings in 1993 within 2 to 5 km of 1992 plantings facilitated comparisons of BWYV incidence for the 2 years.

Two deviations emerged in the 1992 BWYV core area (Figs. 1 and 7): (i) eastern perimeter field 60 just before seed harvest in 1992, and (ii) east central area field 11 in 1993. Field 60, which contained an estimated 50% (10/20) virus-infected plants on 6 May, contained 85% (17 of 20) virus-infected plants just before harvest (24 July; data not included in Figure 2), suggesting a major May–June BWYV-vectoring event. In comparison, 20-plant samples taken from fields 1, 51, and 39 on 24 July were all free of ELISA-detectable BWYV. Measurements of BWYV incidence in field 11 produced two minor surprises: (i) an ostensibly declining BWYV incidence in 1992 (Fig. 7) and (ii) contrasting BWYV season-end BWYV-incidences in adjacent 1992 and 1993 fields: 1992 (40%) and 1993 (87%) (Fig. 9). The apparent decline in BWYV-incidence suggested that infected plants probably became stunted and overgrown by healthy plants, reducing access to them during subsequent sampling. The 1992 and 1993 results suggested maximal BWYV incidence near the Willamette River in the northwestern portion of the sampled area (fields 33, 102, and 70; Fig. 1), with field 11 in January 1992, field 11 locality in June 1993, and field 60 in July 1992 included in the high-incidence zone.

Precipitous increases in BWYV in fields 33 and 102 between the January and February sampling dates (Fig. 7) provided opportunity to test the incidence of BWYV in five weed species commonly infected with the virus and that were potential BWYV-inoculum sources for aphid-vector transmission to sugar beet plants. BWYV was detected in 50 to 90% (field 33) and 33 to 56% (field 102) of the following weed species: *Anthemus cotula* (dog fennel), *Brassica campestris* (field mustard), *Raphanus sativus* (wild radish), *Senecio vulgaris* (groundsel), and *Sonchus oler-*

aceus (common sowthistle). Aphid species that are recognized BWYV vectors and are known to occur on one or more of these weed species in western Oregon (16) include *Aphis gossypii* Glover, *Brevicoryne brassicae* (L.), *Brachycaudus helichrysi* (Kaltenbach), *Macrosiphum euphorbiae* (Thomas), and *Myzus persicae* (Sulzer).

Following the 6 May 1992 sampling of field 11 (Fig. 7), a large weedy area adjacent to the field was sampled to estimate BWYV incidence in known hosts of this virus. BWYV was ELISA-detectable in one of 14 *Amaranthus powellii* (pigweed) plants, in one of two wild radish plants, and in none of three groundsel plants. Despite limited numbers of plants available for sampling, this relatively low incidence of BWYV in these weed hosts corresponded to a low midseason incidence of the virus in adjacent sugar beet seed plants. Pigweed was one of three weed species identified as important hosts of *Myzus persicae* in Washington peach orchards (28).

Pathosystem Relationships in the BWY Disease Cycle

Our attempt to conceptualize four dynamically interacting factors in the BWYV disease cycle is presented in Figure 10. These factors include the virus, seasonal climate changes, coexistent BWYV-susceptible crop and weed species, and indigenous aphid vectors. *M. persicae* is presented because of its well-described phenology (30,32) and its demonstrated role as a BWYV vector (8,30,32,37). Increasing incidence of BWYV in biennial sugar beet seed crops during August to July is depicted as an arrow of increasing width.

Seasonal parameters for *M. persicae* and weed and crop species (Fig. 10) are conservative. During mild winters in the Willamette Valley, aphid vectors (16) survive as adults and eggs on protective, low-lying foliage of overwintering crops and weeds. Likewise, some vegetable crops (spinach, Swiss chard, turnips) can be grown throughout mild winters. Field mustard (*Brassica campestris*) usually persists year-round as successively emerging seedlings, and other annual weed species (groundsel, cut-leaf geranium, and redstem filaree) are capable of similar behavior. Seedlings of both pigweed and prostrate amaranth can emerge in late summer, becoming BWYV-infected soon after emergence and persisting as BWYV inoculum sources into the fall and winter. Pigweed, particularly, is widespread in the valley, where it is a food source for four known aphid vectors of BWYV: *Aphis fabae* Scopoli, *Aphis gossypii*, *Aulacorthum solani* (Kaltenbach), and *Macrosiphum euphorbiae* (16). Canada thistle (*Cirsium arvense*), an introduced deep-rooted perennial that is resistant to herbicidal eradication, exists as extensive plant colonies. Once infected, such colonies could provide a

vast BWYV inoculum reservoir almost indefinitely. Vectors of BWYV known to occur on this species include *Macrosiphum euphorbiae* and *Myzus ornatus* Laing (16). Other persistent, year-round, weedy reservoirs of BWYV inoculum are red clover (*Trifolium pratense*), subterranean clover (*T. subterraneum*), and burdock (*Arctium minus*), from which BWYV potentially could be vectored by *Aphis fabae*, *Aulacorthum solani*, *Brachycaudus cardui* (L.), *B. helichrysi*, *Myzus ornatus*, or *M. persicae* (16).

In essence, the agroecosystem harbors three interdependent, year-round inoculum subreservoirs of BWYV from which at least six known BWYV aphid vector species could disseminate the virus to emerging crop and weed plants. Subject to intrinsic behaviors of aphid vector species, it is plausible that a free multidirectional exchange of BWYV occurs among weeds, sugar beet seed crops, and vegetable crops coexisting in this agroecosystem. With such dynamic interactions, no single BWYV inoculum subreservoir could be considered preeminently causal. Instead, all potentially contribute to an enduring endemicity of BWYV in this distinctive agroecosystem.

Crop Production Coexistent with Endemic BWYV

Fortunately, most vegetable crops in western Oregon are only mildly affected by BWYV, excepting spinach and head lettuce. Other BWYV-susceptible crops either comprise small-scale plantings (e.g., garden beet, Swiss chard, and turnip) or tolerate infection with little effect on yield (e.g., sugar beet seed, radish seed, broccoli, and processing pea). When broccoli and pea crops are infected early, occasional plants may be severely stunted by BWYV, but such plants are typically overgrown by healthy plants and have little effect on crop yields. Plants that become infected after bloom stage usually develop only mild yellows symptoms, persisting until harvest. Similarly, sugar beet plants grown for seed are usually much less affected by BWYV than by limiting edaphic factors, genotype characteristics, or cultural practices. Fields containing 60 to 80% BWYV-infected plants in May produced seed yields in July that were equal to those with 20 to 30% BWYV-infected plants (17). However, BWYV-associated reductions of sugar beet root and sugar yields, when plants became infected by or before April, were reported by Tamaki et al. (31).

Protecting spinach and head lettuce crops against the BWYV-infection process would be challenging and may not be economically feasible. Even when lettuce plants inevitably become infected, however, control of the BWY disease may be possible, either by conventional resistance screening or breeding procedures, or by genetic engineering. Our preliminary

screening of lettuce and spinach cultivars and selections for tolerance to BWYV infection in the Willamette Valley (18) indicated that head lettuce genotypes varied significantly in degree of damage caused by BWYV infection, in agreement with other reports (36,40), and that all spinach genotypes tested were susceptible and severely injured by BWYV infection. The extent to which BWY-tolerant head lettuce genotypes can satisfy production and fresh-market requirements is yet to be determined.

Degrees of BWYV susceptibility among three other *Lactuca* species (*L. saligna* (L.), *L. serriola* (L.), and *L. virosa* Rydb.) were investigated by Maisonneuve et al. (25), with a high level of resistance reported for *L. virosa* selection IVT 280. *Lactuca* resistance to BWYV was attributed to a single dominant gene. Use of this gene through interspecific crosses with *L. sativa* would seem to be plausible.

Questions Deserving Further Investigation

BWYV-like luteoviruses. We believe our proof-testing and application of BWYV polyclonal antiserum established an accurate accounting of BWYV incidence in the western Oregon agroecosystem. Consequently, we are confident in our report of BWYV in 30 plant species. At the same time, we believe we encountered luteoviruses in certain weed species that were completely undetected by our ELISA system. Many shepherd's-purse plants, particularly those occurring as weeds in BWY-damaged lettuce fields, exhibited typical luteovirus symptoms; yet detection of BWYV in these plants was both rare (Table 1) and independent of such symptoms. Shepherd's-purse, in fact, was a favored plant for propagation and purification of BWYV (3) and has been considered a "seemingly universal host for aphids"

(16,19). The presence of luteovirus-like symptoms, with the absence of ELISA-detectable BWYV in this prevalent weed species, suggested the presence of an undetected luteovirus. Likewise, our comparisons among specific luteovirus antisera and luteovirus-reacting monoclonal antibodies produced occasional results suggesting luteovirus mixtures or unresolved virus identities, particularly in field mustard plants. Distinctions between BWYV and such viruses as beet mild yellowing, malva yellows, and turnip mild yellows luteoviruses (39) are still being defined. Thus, further investigations into the western Oregon agroecosystem are required for an understanding of the number and nature of luteoviruses with BWYV-like host ranges. These investigations should include isolation, pathological and molecular-biological characterization, and viral identifications.

BWYV vectors. Finally, too little is currently known about indigenous aphid spe-

Fig. 10. The beet western yellows luteovirus (BWYV) disease cycle in western Oregon depicts the concurrence of BWYV-susceptible crop and weed hosts, and includes life stages of the green peach aphid, *Myzus persicae* (30), a recognized BWYV vector prevalent in western Oregon and the Pacific Northwest. Five other known vectors of the virus occur on one or more of 30 crop and weed hosts of BWYV in western Oregon. Spring aphid flights coincide with spring-sprouting weedy hosts of BWYV and with emerging spring-planted BWYV-susceptible crops. Likewise, late-summer plantings of vegetable and sugar beet seed crops and a continuing emergence of weedy BWYV hosts are refuge to aphids migrating from maturing summer annual crops. These factors interacting with a well-watered environment and mild winters promote both abundant BWYV inoculum and long-season activity of BWYV-vectoring aphid species.

cies and biotypes that are able to transmit BWYV and its relatives among crop and weed species in our described pathosystem. We therefore believe coordinated investigations of luteoviruses and aphid vectors could provide significant new data for a conceptual disease cycle (Fig. 10), including an expansion of our record (16) of aphid species on crops and weeds in western Oregon.

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