Distribution and Incidence of *Iris yellow spot virus* in Colorado and Its Relation to Onion Plant Population and Yield

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ABSTRACT

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Iris yellow spot virus (IYSV) is an emerging and potentially devastating disease of onion that was recently detected in Colorado and other onion producing regions in the western United States. In annual surveys, IYSV was confirmed in one of 18 fields (5.6%) in 2001, four of 24 (16.7%) in 2002, and 41 of 56 (73.2%) in 2003. IYSV was confirmed on volunteer onions in 2003 at all four locations where IYSV was observed in the onion crop the previous year. The disease was detected in six of seven western Colorado onion fields surveyed in 2003, but was not observed any year in southern or northeastern Colorado. The spatial variability of disease incidence, yield, and plant population also was mapped in two fields in 2003 using the global positioning system and a geographic information system. Disease incidence varied among cultivars, plant population, fields, and location in the field. Distinct disease gradients were observed in both fields with susceptible cultivars Teton and Granero, but not in the moderately resistant cultivar Sterling. In fields planted to the susceptible cultivars, disease incidence was highest on the field edges and lowest near the field centers. Plant population was negatively correlated with IYSV incidence in cultivar Sterling ($R^2 = 0.56$, $P = 0.003$), but not with the susceptible cultivars. Yield of jumbo market class onions, but not total yield, was negatively correlated with increasing IYSV incidence ($R^2 = 0.37$, $P = 0.012$) in cultivar Teton. Colossal market class yield, but not other yield components, was negatively correlated with IYSV incidence in cultivar Sterling ($R^2 = 0.28$, $P = 0.061$). The results of these studies indicate the distribution of IYSV is rapidly expanding in Colorado and is associated with a general reduction in bulb size.

Additional keywords: *Allium cepa*, GIS, GPS, *Thrips tabaci*, tospovirus

Onion is a high-value and important crop to Colorado, being produced on 6,000 to 10,000 ha annually, and generating greater than $50 million in farm receipts in 2002 alone (3). Nearly all of the crop is spring planted, either as seed or as transplants. Transplants are produced locally in greenhouses by growers, but are usually field-grown and imported from California, Arizona, or Texas (21). Colorado has four distinct onion growing regions, namely western (west of the Rocky Mountains), southern (concentrated in and adjacent to the Arkansas River Valley), the Front Range (extending from the northern Rocky Mountains eastward approximately 60 km), and northeastern. Each production region is isolated from other regions by 100 to 500 km, and the climate, soils, and production practices often vary among regions (21).

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Iris yellow spot virus (IYSV) is a new tospovirus (6) that has emerged as a potentially devastating and widespread disease of onion (*Allium cepa* L.) in the western United States. Tospoviruses must be acquired by thrips (Thysanoptera: Thripidae) larvae, but only the second larval instars and adults transmit tospoviruses after circulation and replication in the vector (24,26). IYSV is reportedly vectored exclusively by onion thrips (*Thrips tabaci*) (14,17); however, vector specificity and transmission efficiency vary among other thrips species and tospoviruses (25). The competence and efficiency of IYSV transmission by other thrips species or biotypes of *T. tabaci* are unknown.

A putative tospovirus associated with onion seed crops was first reported in the United States in 1993 (11) and later was identified as IYSV (6). The disease was limited to onion and other *Allium* species grown for seed production, and adjacent onion bulb crops were asymptomatic, although leaves of the bulb crop often yielded positive serological results for IYSV (S. K. Mohan, *personal communication*). IYSV was later reported on onion from Israel (9) and Brazil (19,20), iris (*Iris hollandica*) in the Netherlands (6), and lisianthus (*Eustoma russellianum*) and *Hippeastrum hybridium* in Israel (13). In 2001, IYSV was observed in bulb onion crops in Colorado (22), Utah, Idaho, and Washington (8; J. Moyer, *personal communication*). IYSV has since been confirmed in all onion producing states in the western United States, including California, Arizona, New Mexico, and Nevada (J. Moyer, *personal communication*).

The reasons for the sudden dissemination and development of IYSV on onion bulb crops remain unclear. Transmission in onion seed does not appear to be epidemiologically important to disease development (S. K. Mohan and J. Moyer, *personal communication*). Abad et al. (1) reported that two genetically distinct populations of IYSV onion isolates exist in the western United States based upon N gene sequence diversity, and a third subgroup was discovered from isolates infecting chives that may constitute a new distinct tospovirus. The N gene diversity may reflect host or ecological niche specialization. Additionally, the nucleocapsid protein of a Brazilian onion isolate of IYSV was 9.5% divergent from iris strains isolated from the Netherlands, and the isolate also differed in host range (19), again suggesting an ecological differentiation may exist.

The spatial distribution of IYSV in and among onion fields and its association with yield loss are unknown, but this knowledge is essential to developing effective multitactic pest management strategies. Therefore, this study was initiated to: (i) survey the distribution of IYSV among fields in Colorado onion producing regions, (ii) elucidate the spatial variability of IYSV in individual onion fields, and (iii) quantify the relationship of disease incidence to onion yield components (colossal, jumbo, and medium sized bulbs).

MATERIALS AND METHODS

Virus detection. Symptomatic plants were confirmed as positive by double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) according to the manufacturer's instructions (Agdia Inc., Elkhart, IN) in our laboratory with the following modifications. One gram of leaf tissue incorporating characteristic IYSV lesions and surrounding asymptomatic green tissue was frozen in liquid nitrogen and ground to a fine powder with a mortar and pestle. Ten milliliters of extraction buffer (1.3 g of sodium sulfite, 20 g of polyvinylpyrrolidone, 0.2 g of sodium azide, 2.0 g of egg albumin, and 20 g of Tween 20 per liter of phosphate-buffered saline Tween 20 wash buffer, pH 7.4) was then added, and the ground leaf sample was thoroughly mixed. Symptomatic leaves often gave negative DAS-ELISA results if leaf sections were directly homogenized in a 1:10 ratio with extraction buffer according to the manufacturer's instructions, but this modified procedure eliminated those false negatives. Absorbance values at least three times as great as those of the healthy controls were considered positive.

Disease surveys. Disease surveys were conducted annually in all onion producing areas of the state from 2001 to 2003. Within each field surveyed, a V-shaped pattern (approximately 100 to 300 m in length by three beds wide) was walked and plants were visually inspected for characteristic IYSV symptoms, including straw-colored, dry, tan, spindle- or diamond-shaped lesions on the leaves, without or with distinct green centers with yellow or tan borders (Fig. 1). The location of each field was recorded using the global positioning system (GPS). Irrigation method, market class (red, white, or yellow cultivar), and whether the crop was seeded or transplanted were also recorded. At least four symptomatic leaves were collected from each location (except in fields where fewer than four symptomatic plants were observed), placed in resealable plastic bags, and stored on ice during transport to the laboratory. Leaves were kept at 4°C for short-term (<4 days) and –80°C for longer periods of storage. A field was considered positive for IYSV if at least one sample was positive by DAS-ELISA.

2001 Field surveys. In 2001, surveys were conducted after bulb initiation in 18 fields (seven Front Range, six western, three northeastern, and two southern) (Table 1). Twelve fields were visited at least twice between bulb initiation and harvest, but the six western Colorado fields were surveyed only once. An estimated 900 ha were assessed.

2002 Field surveys. In 2002, 24 fields were surveyed in Colorado growing regions, including 10 Front Range, three northeastern, five southern, and six western. Weekly surveys were initiated approximately 2 weeks before bulb initiation and continued until harvest. An estimated 1,200 ha were surveyed.

2003 Field surveys. Fifty-six Colorado fields were surveyed in 2003, including 36 Front Range, three northeastern, 10 southern, and seven western. The four locations in the Front Range production area where IYSV was confirmed in 2002 were surveyed for disease on volunteer onions that developed in and around the 2003 rotational crop. In 2003, the four different fields were cropped to corn (*Zea mays*), alfalfa (*Medicago sativa*), carrot (*Daucus carota*), and dry bean (*Phaseolus vulgaris*). Symptomatic onion volunteers from each location were collected and assayed for the presence of the virus as previously described.

2003 Spatial disease mapping. In two fields with confirmed IYSV infection, disease incidence and onion bulb yield components (prepack, medium, jumbo, colossal, and total yield) were spatially mapped and interpolated. Field 1 was 6.48 ha in area, furrow irrigated, and seeded to the susceptible cultivar Teton. Adjacent to Field 1 was winter wheat (*Triticum aestivum*) on the western and eastern borders, field corn on the southern border, and dry bean on the northern border. Field 2 was 10.12 ha in area, furrow irrigated, and seeded to the susceptible cultivar Granero (east 4.86 ha) and moderately resistant cultivar Sterling (west 5.26 ha). IYSV reaction classification was based upon incidence of symptomatic plants in replicated trials in two grower fields in 2003; these classifications did not consider yield response to disease (H. F. Schwartz and D. H. Gent, *unpublished*). Dry bean was planted along the eastern, sugar beet (*Beta vulgaris*) on the southern and northwestern, field corn on the northeastern, and noncrop land on the western border. The perimeter of each field was mapped by walking the border using a differentially corrected Trimble Ag114 backpack GPS unit (Trimble Navigation Limited, Sunnyvale, CA) equipped with a handheld pen-top-based Fujitzu computer (Tokyo, Japan) and MapInfo Professional v. 6.5 FarmGPS software (MapInfo Corp., Troy, NY). The differentially corrected GPS accuracy was less than 1 m (12).

A 0.40 ha virtual grid and georeferenced random systematic sampling points were superimposed on each field using FarmGPS software. Each point was navigated to and marked with a flag. The plant population and IYSV incidence from a 3-m section of one bed centered on the previously placed flag were recorded approximately 7 days before harvest. Each 3-m plot from field 1 and field 2 cultivar Sterling was mechanically topped and harvested, sorted according to market class (prepack, medium, jumbo, and colossal bulbs) (19), and weighed to estimate yields. Yield data were not available from cultivar Granero in field 2 because the cooperating grower harvested this portion before the plots could be removed. Spatial variability of IYSV incidence, plant population, and market class and total onion yield were interpolated in FarmGPS software using inverse distance weighting to create thematic maps based upon natural classification breakpoints.

Statistical analysis. The relationship between IYSV incidence, plant population, and market class and total yield were quantified by simple linear regression in SAS v. 8.1 (PROC REG, SAS Institute Inc., Cary, NC). The influence of each point was quantified using Cook's Distance (*Di*), considering an observation relatively influential if $Di > 0.50$ and highly influential if $Di > 1.00$ (18). An alpha of 0.1 was used as the level of significance because onion yields are known to vary widely within a given field (R. Khosla, *unpublished data*), and type II errors were deemed to be less important than type I errors in this study. Observational data from multiple locations have strongly suggested a relationship exists between IYSV incidence and yield (H. F. Schwartz and D. H. Gent, *unpublished*), and rejection of this research hypothesis in favor of a null hypothesis (a relationship does not exist between IYSV incidence and yield) is therefore assumed to be a more serious error. Moran's I spatial autocorrelation coefficient was used to determine the spatial structure of IYSV incidence and onion yield components. Moran's I is a measure of spatial autocorrelation used to infer spatial dependence and is directly analogous to Pearson's correlation coefficient (16). Data are considered positively spatially dependent (clustering of similar observations in space) if $I > -1/(n-1)$, negatively spatially dependent (neighboring observations dissimilar in space) if $I < -1/(n-1)$, and spatially independent (observations random in space and do not depend on neighboring observations) if $I = 0$. Spatial gradients across fields were quantified by covariance analysis of Universe Transverse Mercator (UTM) easting and northing coordinates and IYSV incidence observations using a

Table 1. Incidence of *Iris yellow spot virus* (IYSV) among Colorado onion fields surveyed from 2001 to 2003

	Fields surveyed for IYSV (no. positive)[z]		
Region	**2001**	**2002**	**2003**
Front Range	7 (1)	10 (4)	36 (35)
Northeastern	3 (0)	3 (0)	3 (0)
Southern	2 (0)	5 (0)	10 (0)
Western	6 (0)	6 (0)	7 (6)
Total surveyed (% positive)	18 (5.6%)	24 (16.7%)	56 (73.2%)

[z] A field was considered positive if at least one IYSV symptomatic leaf was positive by a double antibody sandwich enzyme-linked immunosorbent assay.

spatial weights matrix and the bimoran I test statistic. All spatial statistics were performed in S-PLUS v. 6.1 (Insightful, Inc., Seattle, WA).

RESULTS

Disease surveys. Characteristic IYSV lesions were observed and confirmed in one out of 18 fields (5.6%) surveyed in the Front Range production region in 2001. These symptomatic onions originated from greenhouse-produced transplants and were organically produced under center-pivot irrigation; this field was the northernmost onion field planted that year. In 2002, IYSV was observed and confirmed from four of 24 fields (16.7%) surveyed in the Front Range production region. Of these four fields, three were furrow irrigated and one was drip irrigated. These positive fields were located within 30 to 35 km of the 2001 positive field and encompassed a 25 km^2 area. In neither 2001 nor 2002 was IYSV detected in northeastern, southern, or western Colorado. Results are summarized in Table 1.

In 2003, however, IYSV was widespread in western Colorado and Front Range production regions. Symptomatic plants were observed in six of seven onion fields (85.7%) surveyed in western Colorado in 2003 and yielded positive serological results for IYSV. These fields encompassed two isolated areas of approximately 400 and 150 km^2 separated by 50 km of noncrop land. In the Front Range production region, IYSV symptoms were observed on plants from 35 of 36 fields (97.2%) surveyed. These fields encompassed approximately 1,600 km^2. Additionally, symptomatic volunteer onions were found in 2003 at all four locations where IYSV was confirmed in 2002 (Fig. 2). IYSV symptomatic volunteer onions were found growing in alfalfa, carrot, corn, and dry bean crops under center-pivot (alfalfa and corn), drip (dry bean), and furrow (carrot) irrigation.

2003 Spatial disease mapping. Limited evidence of positive spatial dependence of IYSV incidence was detected in this study with random systematic sampling on a 0.40 ha grid. Moran's I spatial autocorrelation coefficient for IYSV incidence was 0.02 (P = 0.05) and 0.10 (P < 0.0001) in fields 1 and 2, respectively, indicating a significant but low degree of positive spatial dependence of IYSV incidence across the fields. Spatial autoregression of IYSV incidence and jumbo (field 1) or colossal (field 2) onion yield were not significant by the likelihood ratio test (P = 0.46 and P = 0.92, respectively), indicating an absence of spatial dependence among yield and IYSV incidence. Variograms were not expected to be informative in the absence of high degrees of detectable spatial dependency and were not constructed.

Geospatial mapping of IYSV incidence in the fields revealed distinct edge effects and disease gradient patterns in both fields (Figs. 3 and 4). In field 1, the highest incidence of IYSV (greater than 80% disease incidence) was observed along the northern and western edges. The western edge of the field was adjacent to a winter wheat crop and tangential to the prevailing westerly wind direction. Disease incidence decreased across the field from the western

Fig. 1. Foliar symptoms of *Iris yellow spot virus* on onion.

Fig. 2. Foliar symptoms of *Iris yellow spot virus* on volunteer onion in alfalfa.

to eastern edge and was lowest in the center of the field (40 to 13% disease incidence). Covariance analysis of UTM easting (longitudinal) coordinates and IYSV incidence by a spatial weights matrix and bimoran I test statistic revealed a disease gradient across the field (bimoran I = –0.09, P = 0.003). In field 2, the highest disease incidence (90 to 100%) was observed in the susceptible cultivar Granero on the eastern edge of the field directly adjacent to a dry bean crop; disease incidence varied from 67 to 100% at the sampling sites with a mean of 90.1%. IYSV incidence was lowest in the moderately resistant cultivar Sterling (27%) along the western edge of the field adjacent to non-crop land (greater than 100 m wide); disease incidence varied from 27 to 70% at the sample sites with a mean of 57.3%. Analysis of variance indicated significantly more disease in Granero than in Sterling (t test F = 9.74, P = 0.0004), but this difference may have been related to a gradient of primary inoculum from an unidentified source rather than cultivar disease resistance. Differences in IYSV incidence were apparent in the onion rows directly along the border between cultivars Granero and Sterling, suggesting cultivar resistance was partially associated with the spatial disease pattern. The bimoran I test statistic revealed a directional disease gradient (bimoran I = 0.09, P < 0.001) of the same magnitude, but in the opposite direction, as field 1.

Total yields of cultivars Teton in field 1 and Sterling in field 2 were not significantly associated with IYSV incidence (Table 2, Figs. 5 and 6). IYSV incidence was negatively associated with jumbo yield in cultivar Teton (R^2 = 0.37, P = 0.012) and explained 37% of the variability in jumbo yield. Other yield components were not associated with IYSV incidence. In the moderately resistant cultivar Sterling, IYSV was negatively associated with colossal yield (R^2 = 0.28, P = 0.061), explaining 28% of the variability. No other yield component was significantly associated with IYSV incidence.

The relation of plant population and IYSV incidence also was studied by simple linear regression. IYSV incidence was negatively associated with plant population in cultivar Sterling (R^2 = 0.56, P = 0.003), but not in cultivars Granero (R^2 = 0.05, P = 0.48) or Teton (R^2 = 0.03, P = 0.54) (Fig. 7). The relation of plant population and IYSV incidence was described by the linear function $y = -0.9144x + 97.043$, where plant population is the independent predictor and IYSV incidence is the dependent response variable. One observation in the northeastern corner of the field where disease incidence was the highest in cultivar Sterling (IYSV incidence = 61%, plant population = 64 plants per 3 m of one bed) was highly influential in the model (Di = 1.28). When removed and refitted, the model $y = -1.24x + 108.82$ was highly significant (R^2 = 0.80, P < 0.0001) and plant population explained 80% of the observed variability in IYSV incidence. No subsequent observations were relatively or highly influential in this second model.

DISCUSSION

The distribution of IYSV on onion in Colorado has increased dramatically since 2001, and has spread rapidly through two onion-growing regions of the state. In 2 years, the disease has spread from a single

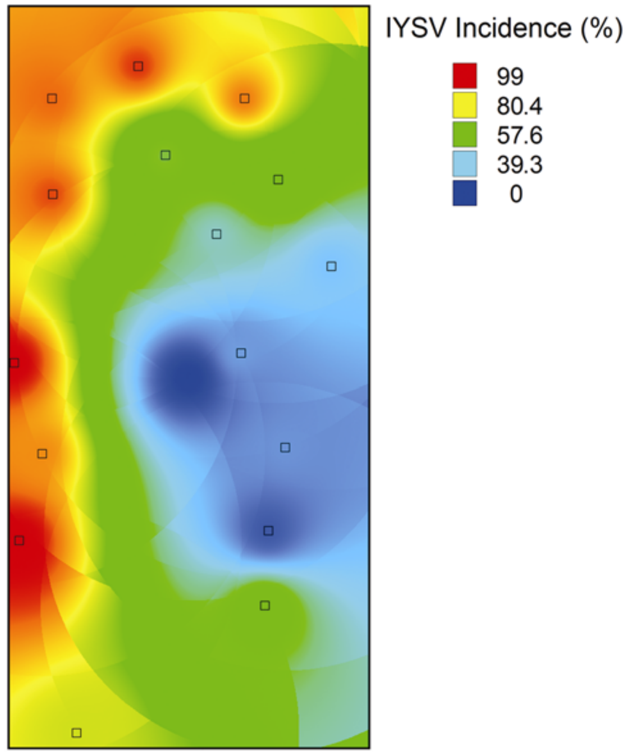

Fig. 3. Spatial variability of *Iris yellow spot virus* (IYSV) incidence (percent infected plants per 3 m of one bed) in an onion field seeded to the susceptible cultivar Teton. Boxes represent random systematic sampling points on a 0.4-ha grid. The thematic map was generated by inverse distance weighting using natural classification breakpoints.

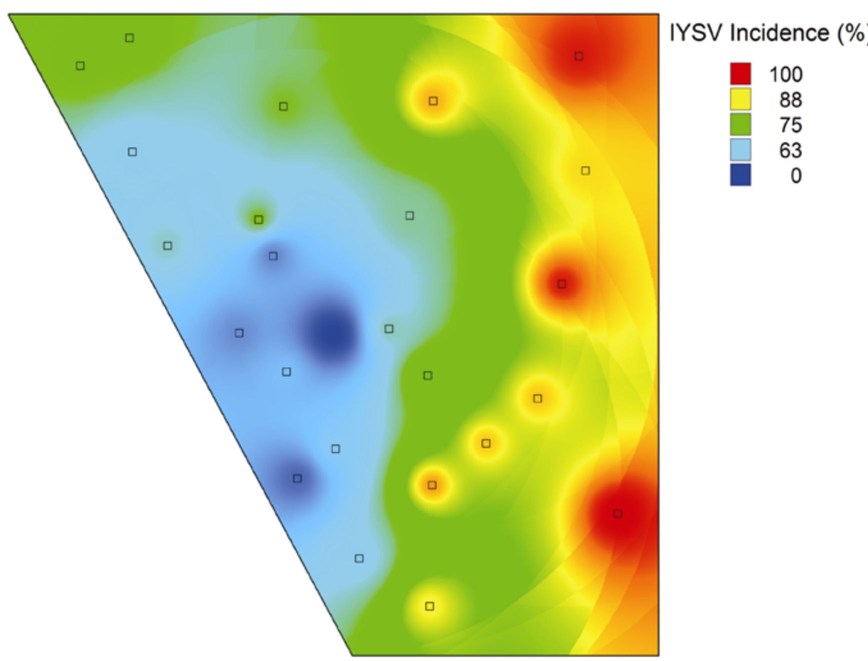

Fig. 4. Spatial variability of *Iris yellow spot virus* (IYSV) incidence (percent infected plants in 3 m of one bed) in an onion field seeded to the moderately resistant cultivar Sterling (left) and susceptible cultivar Granero (right). Boxes represent random systematic sampling points on a 0.4-ha grid. The thematic map was generated by inverse distance weighting using natural classification breakpoints.

field in northern Colorado to nearly all fields surveyed in the Front Range production region in 2003, and has become an immediate and serious threat to onion production. However, the disease may have been present at a low level prior to 2001. IYSV-like symptoms were observed in one onion field in 1999 in the northern Front Range production region, but the pathogen was not isolated and positively identified. The occurrence of IYSV in western Colorado in 2003 is significant, but the inoculum source(s) is unknown. Western Colorado is separated from other onion production regions of the state by the Rocky Mountains, a significant barrier to vector dispersal. Although IYSV was confirmed in western Colorado, it has not been observed in northeastern or southern Colorado as of 2003.

In this study, we document for the first time the occurrence of IYSV on volunteer onion. At all locations where the disease was observed the previous year, we confirmed IYSV on volunteer onion growing in ensuing dry bean, alfalfa, field corn, and carrot crops. Symptomatic volunteer onions were observed in a variety of crops with various irrigation methods (center pivot, furrow, and drip), and may provide a biological bridge between onion crops in Colorado. The means by which the volunteers become infected is uncertain. IYSV apparently is not present, or detectable, in onion bulbs or roots (14), and a direct effect on bulbs has not been reported. Volunteers may be infected after emergence early in spring by viruliferous thrips associated with the bulbs. Adult thrips remain viruliferous for their entire life (26) and can overwinter in association with onion bulbs and debris (7). It is also possible that volunteers emerge free of IYSV, but are subsequently infected by viruliferous thrips migrating from an infected winter annual or perennial alternate host. In this study, IYSV incidence was very high (nearly every plant) on volunteer onions at each location, and disease symptoms were observed before disease was detected in the seeded or transplanted onion crop. This suggests there may be a carryover of IYSV in infected bulbs or viruliferous thrips overwintering in association with the onion bulbs.

The reasons for the absence of disease in northeastern and southern Colorado are unclear, but we expect IYSV will eventu-

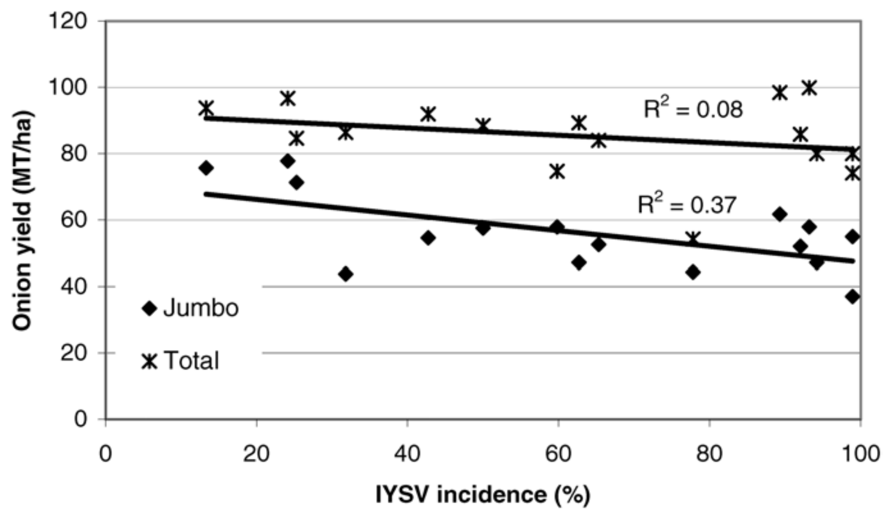

Fig. 5. Relation of *Iris yellow spot virus* (IYSV) incidence to total and jumbo market class yield of onion cultivar Teton. Colossal-sized onions were rarely observed and were included with jumbo-sized onions. IYSV incidence and total yield were not significantly associated, but IYSV incidence and jumbo market class yield were significantly associated, (R^2 = 0.37, P = 0.012).

Table 2. Parameter estimates and significance of predictor variables of onion yield components and *Iris yellow spot virus* (IYSV) incidence in the susceptible cultivars Teton and Granero and moderately resistant cultivar Sterling

Cultivar Response variable[x]	Parameter[y]	Parameter estimate[z]	$P > \|t\|$	Model R^2	Model F value	Model $P > F$
Teton						
Prepack	Intercept	11.40	0.28	0.06	0.83	0.38
	IYSV	0.13	0.38			
Medium	Intercept	179.09	3.70	0.05	0.78	0.39
	IYSV	0.62	0.89			
Jumbo	Intercept	632.46	<0.0001	0.37	8.26	0.01
	IYSV	–2.10	0.01			
Total	Intercept	822.07	<0.0001	0.08	1.24	0.28
	IYSV	–0.98	0.28			
IYSV	Intercept	115.55	0.18	0.03	0.40	0.54
	Population	–0.49	0.54			
Sterling						
Prepack	Intercept	–1.86	0.91	0.05	0.58	0.46
	IYSV	0.21	0.46			
Medium	Intercept	21.61	0.57	0.14	1.78	0.21
	IYSV	0.83	0.21			
Jumbo	Intercept	482.29	0.24	0.15	1.27	0.28
	IYSV	–3.56	0.28			
Colossal	Intercept	114.61	0.02	0.28	4.35	0.06
	IYSV	–1.41	0.06			
Total	Intercept	623.65	0.009	0.11	1.42	0.26
	IYSV	–3.94	0.26			
IYSV	Intercept	96.72	<0.0001	0.56	13.97	0.0033
	Population	–0.91	0.0033			
Granero						
IYSV	Intercept	97.00	<0.0001	0.05	0.55	0.48
	Population	–0.13	0.48			

[x] Yield data were not available for Granero.
[y] IYSV = IYSV incidence (percent infected plants); population = number of onion plants per 3 m of one bed.
[z] Regression coefficients determined by simple linear regression $Y = \alpha + \beta X$; X = predictor variable, Y = response variable.

ally be introduced into these regions in the future. Approximately 10 to 15% of the Colorado onion crop is grown from transplants, generally produced in and subsequently imported from southern Arizona and California; IYSV has been confirmed from both of these regions (J. Moyer, *personal communication*). Onion transplants often harbor *T. tabaci* when they arrive in Colorado, and these thrips are often resistant to registered onion insecticides (23). Therefore, infected plants from a region(s) where disease was present may be an epidemiologically important inoculum source. Pathogen dispersal on other hosts (such as ornamental) into these regions also cannot be disregarded. The first confirmed report of IYSV in Colorado in 2001 was in an onion field planted to greenhouse-produced transplants grown alongside ornamental plants (22). The ornamentals may have been asymptomatically infected when introduced into the greenhouse and served as the subsequent inoculum source for the onion transplants. Studies are ongoing to elucidate long-distance IYSV dispersal mechanisms.

The relation between IYSV incidence and onion yield components revealed that bulb size, but not total yield, was associated with disease incidence. Jumbo and colossal onion yield components were negatively correlated with IYSV incidence in the susceptible cultivar Teton and moderately resistant cultivar Sterling. Onion yields vary widely across fields in the absence of disease, and even the detection of treatment effects between untreated and high nitrogen fertilization rates is often difficult (R. Khosla, *unpublished*). In light of this variability in onion yield, the ability to explain 28 and 37% of colossal and jumbo onion yields is notable. The variability in plant population observed in this study was not associated with yield (data not presented). Correspondingly, plant population and IYSV incidence failed to predict total onion yield in multiple linear regression models.

Plant population was strongly associated with IYSV in the moderately resistant cultivar Sterling, but not in the two susceptible cultivars. Dense plant populations and crop canopy architectures consistently reduce *Tomato spotted wilt virus* (TSWV) incidence in peanut (4), apparently because thrips cannot locate individual plants and land on leaf surfaces less often. A similar phenomenon may exist in IYSV of onion with moderately resistant cultivars. In susceptible cultivars such as Teton and Granero, thrips may land and feed less often in a dense plant population; but the plants may become symptomatic even with low virus titers. Conversely, high virus titers or thrips populations in areas of lower plant populations may have overcome the limited resistance in cultivar Sterling. Host preference was not quantified in this study, but may be a component of IYSV transmission and/or host disease resistance. However, Al-dosari (2) found little or no thrips feeding preference among onion cultivars in Colorado, but large differences in onion cultivar tolerance to thrips feeding injury. The cultivars included in this study may vary in their tolerance to thrips feeding, and onion cultivar IYSV disease reaction (i.e., moderately resistant, susceptible) is likely the result of an interaction among host genetic resistance to the pathogen, virus titer, tolerance to thrips feeding injury, and thrips host preference. Neither partial host resistance to the disease nor plant population alone effectively reduced disease incidence, suggesting that a complete integrated approach is necessary for successful IYSV and thrips management.

Within fields we intensively sampled and analyzed by spatial statistics, we found limited evidence of positive spatial autocorrelation in IYSV incidence and no evidence of autocorrelation among yield components. This is consistent with TSWV in other cropping systems (5,10) and suggests limited secondary spread of IYSV occurs within a field. However, we used a 0.4-ha random systematic sampling grid, which may not be sufficient to detect spatial dependence of disease incidence or yield at a scale less than 0.4 ha. Spatial autocorrelation generally decreases with distance between two binary variables (27), but the rate of autocorrelation decline with distance varies depending on disease incidence. Disease incidence was relatively high across both fields studied and may improve the power of spatial autocorrela-

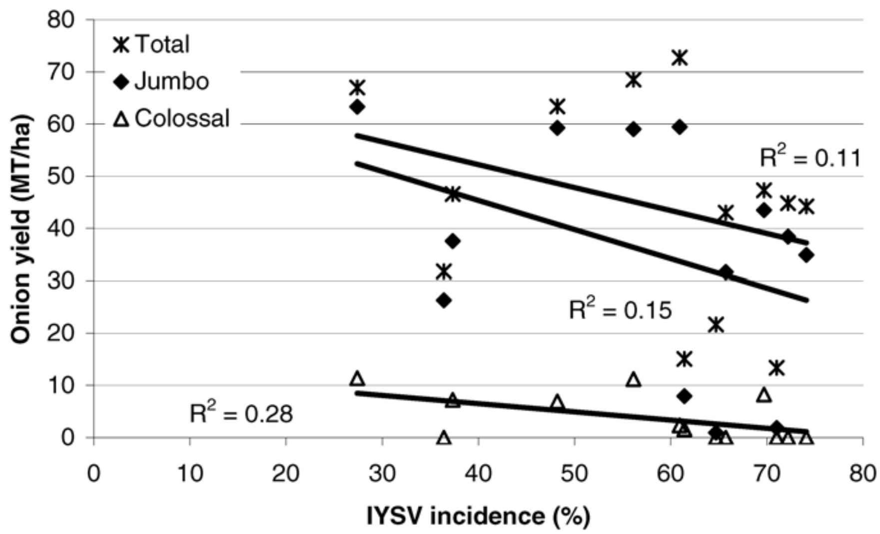

Fig. 6. Relation of *Iris yellow spot virus* (IYSV) incidence to total, colossal, and jumbo market class yield of onion cultivar Sterling. IYSV incidence and total or jumbo yield were not significantly associated, but IYSV incidence and colossal market class yield were significantly associated (R^2 = 0.28, P = 0.061).

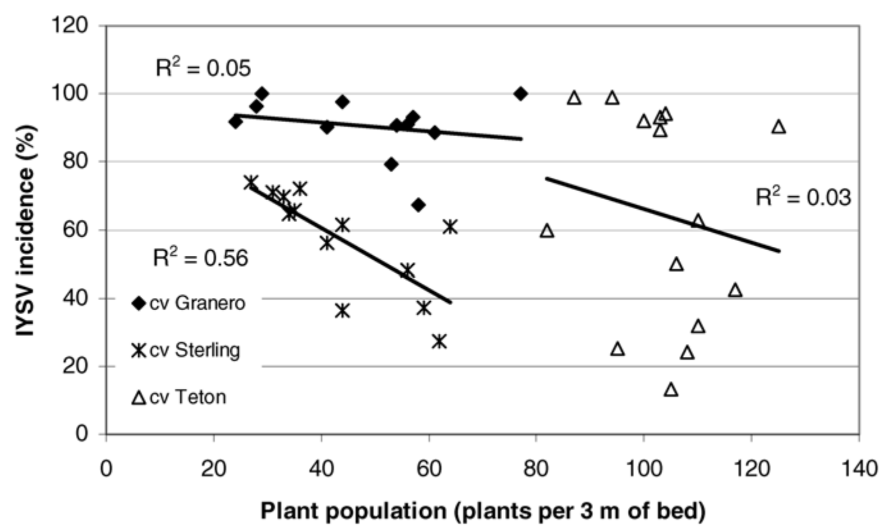

Fig. 7. Relation of plant population to *Iris yellow spot virus* (IYSV) incidence in onion cultivars Sterling (P = 0.003), Granero (P = 0.48), and Teton (P = 0.54).

tion statistics at large sampling scales (27). Future studies of IYSV and yield spatial distribution will incorporate cluster sampling at various scales to determine the range of spatial dependence. Distinct edge effects and disease gradients were observed in both fields, but were not solely explained by prevailing wind direction or neighboring crop. Disease gradients originating from field borders have been reported with TSWV in tomato (*Lycopersicon esculentum*) and pepper (*Capsicum annuum*), but most infections arose from primary transmission; secondary disease spread was limited (10).

The spatial distributions of virus-infected plants are often varied and influenced by several factors, including environmental conditions and vector dispersal (15). The epidemiological basis for the disease patterns observed in this study is unclear, but cultivar resistance in other pathosystems has not affected spatial or temporal disease development patterns (5). IYSV spatial distribution may be related to edaphic soil characteristics such as salinity, texture, and organic matter content. Preliminary data suggest IYSV may be associated with plant stress, such as moisture and temperature extremes, compaction, and soilborne diseases such as pink root (caused by *Phoma terrestris*). The relation of biotic and abiotic soil properties to IYSV incidence and distribution are currently under investigation.

In this study, we have established the relation of IYSV to yield, plant population, and spatial structure within fields, in addition to documenting the rapid dissemination of IYSV through two Colorado onion production regions and its association with volunteer onion. However, many epidemiological and management questions remain. How is IYSV disseminated over long distances? What is the role of volunteer onion in IYSV epidemics? What factors influence the spatial and temporal structure of IYSV epidemics among fields? Are the effects of combined management strategies such as partial host resistance, crop rotation, sanitation, origin of seed or transplants, and agronomic practices additive or synergistic? These and other research questions are currently under investigation and will be critical to developing effective and economical management strategies for IYSV of onion.

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