POPULATION ECOLOGY

Spatial and Temporal Dynamics of Potato Tuberworm (Lepidoptera: Gelechiidae) in the Columbia Basin of the Pacific Northwest

S. J. DEBANO,[1,2] P. B. HAMM,[1] A. JENSEN,[3] S. I. RONDON,[1] AND P. J. LANDOLT[4]

Environ. Entomol. 39(1): 1–14 (2010); DOI: 10.1603/EN08270

ABSTRACT A landscape-scale study from 2004 to 2006 investigated the spatial and temporal dynamics of a new pest to the Columbia Basin of the Pacific Northwest, the potato tuberworm, *Phthorimaea operculella* (Zeller). Male *P. operculella* were monitored in spring, summer, and fall each year with a pheromone-baited trapping network in Oregon and Washington. The objectives of the study were to (1) describe the temporal and spatial dynamics of the recent outbreak of *P. operculella* in the region and (2) examine the relationship of the spatial and temporal distribution of the outbreak and weather (air temperature, precipitation, and dew point) and geographic variables (elevation and latitude). Weather data during the *P. operculella* outbreak were compared with a reference period (1993–1999) that occurred before the outbreak. The outbreak in 2004, which caused the first widespread tuber damage in the region, was positively associated with warmer temperatures in the preceding fall and in the spring, summer, and fall of the growing season. October and November 2003 and March 2004 were also drier than the reference period. However, the winter of 2003/2004 was colder than the reference period and thus mild winter conditions did not explain the outbreak. The importance of environmental variables on the seasonal spatial distribution of the pest each year was examined using nonparametric multiplicative regression. Locations with higher spring, summer, or fall temperatures were associated with increased trapping rates in most seasons. Elevation and latitude seemed to play a constraining role, because low trapping rates of *P. operculella* were associated with higher elevations and latitudes.

KEY WORDS *Phthorimaea operculella*, Columbia Basin, pheromone-baited traps, population dynamics, spatial distribution

The potato tuberworm, *Phthorimaea operculella* (Zeller), is one of the most economically significant insect pests of cultivated potatoes (*Solanum tuberosum* L.) in tropical and subtropical regions (Trivedi and Rajagopal 1992, Sporleder et al. 2004). Although its origin has long been a source of speculation (Graf 1917, Trivedi and Rajagopal 1992), it is commonly believed to have originated in South America (Radcliffe 1982, Briese 1986, Sporleder et al. 2004). Since the 1800s, *P. opercullela* has achieved a worldwide distribution that includes portions of the United States, where it was first documented in California in 1856 (Graf 1917). In 1873, *P. operculella* was collected in Texas, and by the mid 20th century, it had been reported in many states with latitudes below 40° N, including Florida, South and North Carolina, Virginia, Maryland, Washington DC, Colorado, and Hawaii (Chittenden 1913; Graf 1917; Underhill 1926; Poos and Peters 1927; Langford 1933, 1934). Within the United States, the most severe damage has been associated with populations in southern California (Chittenden 1913, Bacon 1960, Shelton and Wyman 1980).

Recently, *P. operculella* emerged as a significant pest of potatoes in the Columbia Basin of Oregon and Washington (Jensen et al. 2005, Rondon et al. 2007), a highly productive potato-growing region of the Pacific Northwest that accounts for ≈20% of U.S. potato production (Johnson et al. 1997). In 2002, a specimen collected by a Washington potato grower was positively identified as *P. operculella* by Washington State University Extension. The first significant economic damage to potato crops in the Columbia Basin region occurred in that same year, when a field in Oregon showed high levels of tuber damage associated with *P. operculella* (Rondon et al. 2007), and by 2003, the pest was a major concern to all growers in the region after potatoes from several fields were rejected by processors or fresh packers because of tuber damage. Since that time, *P. operculella* has cost growers in the Columbia Basin millions of dollars through increased pesticide application and unmarketable potatoes (Rondon et al. 2007).

Although the recent outbreak is the first report of major, widespread damage caused by *P. operculella* in the region, several lines of evidence suggest that *P. operculella* is not new to the Pacific Northwest. Chit-

---

[1] Oregon State University, Hermiston Agricultural Research and Extension Center, Hermiston, OR 97838.

[2] Corresponding author, e-mail: sandy.debano@oregonstate.edu.

[3] Washington State Potato Commission, Moses Lake, WA 98837.

[4] USDA–ARS, Yakima Agricultural Research Laboratory, Wapato, WA 98951.

tenden (1913) recorded its presence in Seattle, Auburn, and Yakima, WA, in the early part of the 20th century; however, he makes no statements concerning the degree of tuber damage associated with the pest or whether it was believed to have been brought into the area from elsewhere. Washington State University's James Entomological Collection has a series of 21 specimens of *P. operculella,* with a label on one for Yakima, WA, dated 18 June 1920 (the other specimens are unlabeled). There are also three *P. operculella* specimens present in the arthropod collection of Oregon State University (OSAC Accession 238) from 1951, with a note on the label stating "in lab on potatoes." It is unclear whether the specimens were collected in potato fields, were associated with tuber damage, or whether they were transported from elsewhere. In addition, an article published in the *Idaho Statesman* newspaper in 1946 describes a *P. operculella* infestation in Cassia County, ID, caused by the import of infected California potatoes to a processing plant in Burley. The article quotes W. Kellogg, "acting director of plant industry," as stating "the tuber moth is in Burly by the millions." However, the only other evidence of *P. operculella* in Idaho in the 20th century are nine specimens in the W. F. Barr Entomology Museum at the University of Idaho collected from stored potatoes in Boise, ID, in 1959. The lack of more substantial reports and collections of *P. operculella* in the Pacific Northwest suggests that populations did not represent any serious threat to potato production in the area. There are no published accounts of potato damage associated with *P. operculella* in the Pacific Northwest in the scientific literature previous to the current outbreak.

The recent *P. operculella* outbreak in the Columbia Basin represents the most extreme northern or southern latitude of a reproducing population of *P. operculella* recorded in the literature. Understanding what factors may have contributed to this outbreak in the Pacific Northwest is vital for understanding the risk this pest poses to growers in the region and for developing effective control methods. This study involved a 3-yr landscape-scale monitoring program of *P. operculella* in the Columbia Basin. Our objectives were to (1) describe the temporal and spatial dynamics of the recent outbreak of *P. operculella* in the region and (2) examine the relationship of the spatial and temporal distribution of *P. operculella* with weather and geographic variables.

Materials and Methods

Pheromone-Baited Trapping Network. The Columbia Basin *P. operculella* trapping network was coordinated by the Oregon State University Extension and the Washington State Potato Commission in the Columbia Basin of Oregon and Washington (Fig. 1) from May 2004 to November 2006. We used white Trécé Pherocon VI pheromone-baited delta traps with removable sticky liners. During the potato growing season the full set of traps were used, whereas a subset of traps in Oregon was used during the winter months of 2004/2005 and 2005/2006. The traps were either suspended from 76-cm pieces of heavy-gauge aluminum wires shaped as "L"s, which were inserted into PVC or metal pipe stands or from PVC elbows connected to PVC-pipe stands. Traps were suspended ≈30 cm above the canopy of the existing vegetation or bare ground. Each trap contained one lure produced at the USDA–ARS Yakima Agricultural Research Laboratory in Wapato. Lures consisted of a rubber septum pre-extracted with methylene chloride and loaded with a 1:1 ratio of E4,Z7–13:Ac and E4,Z7,Z10–13:Ac. The pheromone load per septum was 100 μg plus 6 mg of BHT in 200 μl of methylene chloride. Traps were monitored weekly; liners were replaced, and the number of *P. operculella* males recorded for each trap. Lures were changed every 4–5 wk in the growing season and every 6 wk in the winter. The geographic coordinates of all trap locations were determined with handheld global positioning units. Traps were typically a short distance away from irrigated crop circles (0.05 ± 0.02 km) and roads (0.58 ± 0.07 km). Although all traps were located in the Columbia Basin potato production region, we did not attempt to quantify the distance of each trap to potential potato sources, both because of the diversity of those sources (e.g., fields planted in potato, fields recently harvested with potatoes left in the soil, cull piles, processing plants, storage facilities) and the temporal variability in their availability (e.g., changes in crop rotation from year to year in a particular field).

Table 1 lists the number of traps located in each state, the date trapping was initiated, the date of full deployment, and the last date of the extended trapping network for each year. In 2004, 102 traps were operating under full deployment in the growing season and nine traps were monitored in Oregon during the 2004/2005 winter season. In the 2005 growing season, 234 traps were operating under full deployment; traps placed in Oregon remained in the exact same locations as the previous year (with five additional traps deployed), whereas the specific locations of all Washington traps differed between 2004 and 2005 because of logistical issues. The changes in location from 2004 and 2005 were relatively small (Fig. 5) and are not expected to impact results. In the 2005/2006 off-season, 11 traps were monitored in Oregon. In 2006, 222 traps were operating during full deployment, with 184 of the 187 trap sites sampled in Washington and all of the Oregon traps in the exact same locations as the previous year.

To examine temporal trends, trapping sites were divided into three general regions based on latitude (Fig. 1). Trapping sites located south of 46°04′ N were characterized as lower Columbia Basin sites and included all trapping sites in Morrow and Umatilla Counties in Oregon and Klickitat County in Washington and trapping sites in southern Benton County in Washington. Trapping sites north of 46°04′ N but south of 46°54′ N were characterized as middle Columbia Basin sites and were located in Washington; these included all trapping sites in Walla Walla and Franklin Counties, northern sites in Benton County,

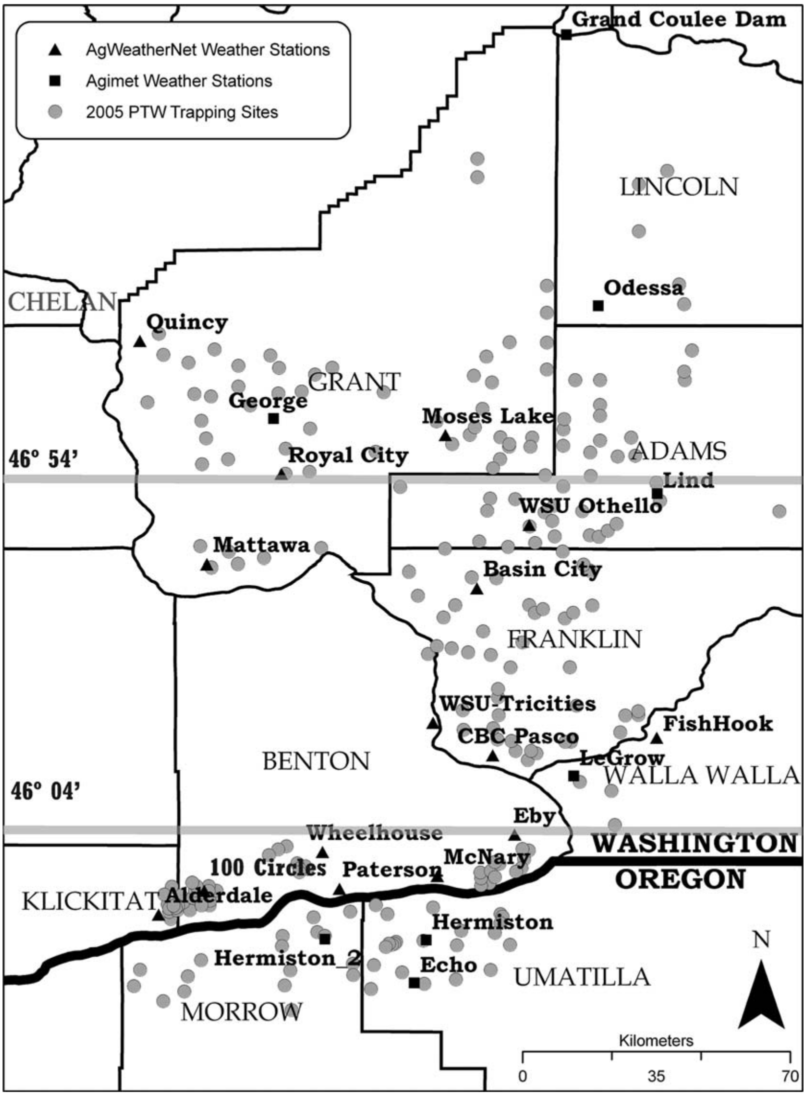

Fig. 1. Map of the Columbia Basin potato production region in Oregon and Washington with locations of 2005 *P. operculella* trapping sites and Agrimet and AgWeatherNet stations. Gray horizontal lines divide the lower, middle, and upper Columbia Basin trapping regions; see text for details.

and southern sites in Grant and Adams Counties. Trapping sites north of 46°54′ N were characterized as upper Columbia Basin sites and included Washington trapping sites in northern Grant and Adam Counties and all sites in Lincoln and Chelan Counties. In the lower, middle, and upper Columbia Basin regions, there were 41, 30, and 31 trapping sites in 2004, respectively; in 2005, there were 89, 75, and 70 traps, respectively; and in 2006, there were 80, 73, and 69 traps, respectively.

Table 1. No. traps and dates of activity for the extended trapping network in 2004, 2005, and 2006

Year	No. traps in full deployment	Date trapping began	Date of full deployment[a]	Date extended trapping efforts ended[b]
2004	102 (35 in OR, 67 in WA)	14 May	28 May	22 Nov.
2005	234 (40 in OR, 194 in WA)	10 Mar.	25 April	30 Nov.
2006	222 (35 in OR, 187 in WA)	23 Mar.	15 April	14 Oct.

[a] Full deployment occurred when all traps to be used in the growing season were operational.
[b] Extended trapping efforts ended when all traps except for those operating through the winter were removed.

Characterizing Weather Conditions During Outbreak. Because *P. operculella* is primarily found in tropical and subtropical areas, we hypothesized that its relatively sudden appearance and establishment as a serious pest of potatoes in the Columbia Basin in 2004 might be caused by changes in weather conditions. To study patterns in weather conditions that may have coincided with the outbreak of *P. operculella,* we examined temperature, precipitation, and dew point from data collected at a weather station at the Hermiston Agricultural Research and Extension Center, a location near some of the most severe infestations. Historical data from 1993 were available. We examined average daily temperature for summer and fall; however, we used minimum daily temperature for winter and maximum daily temperature for spring because we hypothesized that these extremes would be more likely to impact *P. operculella* numbers than average temperatures for those seasons. Cold temperatures in winter are most likely to impact *P. operculella* populations in temperate areas through effects on mortality (Doğramaci et al. 2008), not developmental rate, and thus mean minimum daily temperature gives the best estimate of environmental factors likely to increase mortality. Maximum temperature in spring is particularly important because fairly short periods of warm weather in an otherwise cool spring can lead to emergence and/or activity of adults, including mating and ovipositing. We calculated the monthly means for each variable for a 6-yr period occurring 3 yr before any documented collection of *P. operculella* in the area (1993–1999) and generated 95% confidence intervals for each monthly average. We then calculated the monthly mean for each variable for those months in 2003/2004, 2004/2005, and 2005/2006 to determine whether those means fell within the 95% confidence intervals for 1993–1999.

Spatial Distribution of *P. operculella*. The spatial distribution of *P. operculella* infestation in the Columbia Basin was mapped using ArcGIS Desktop Arc View 9.2 (Environmental Systems Research Institute, Redlands, CA); georeferenced trapping data were plotted for three seasons each year, except for spring 2004, when only 2 wk of data were available. Each season was comprised of 3 mo: spring (March, April, May); summer (June, July, August); and fall (September, October, November). The mean number of males per week for each trap for each season was calculated and classified into one of four categories: 0, 1–30, 31–60, and >60 males per week for visualization.

Relating Spatial Distribution to Environmental Variables. We used Hyperniche Version 1.0 (McCune and Mefford 2004) to study the relationship of environmental variables and the mean number of male *P. operculella* per trap in each season of each year with nonparametric multiplicative regression. This approach is better suited to address questions concerning species responses to environmental variables than other commonly used models that are additive and often assume linear or sigmoid response shapes (e.g., multiple linear regression or logistic regression) (McCune 2006a). Because many species show hump-shaped responses to environmental gradients and their responses to one factor often depend on other factors (i.e., factor interactions are expected), traditional regression techniques are not appropriate. As McCune and Mefford (2004) pointed out, the limitations of using these traditional techniques is magnified when examining species responses to multiple environmental variables—as the number of variables increases, the potential interaction terms increase exponentially (Scott 1992). Unlike traditional regression approaches, nonparametric multiplicative regression effectively models species responses to multiple environmental variables using nonparametric curve-fitting techniques, with the effect of each variable depending on the value of other variables (McCune 2006a). Instead of arriving at a global model, in which coefficients are derived in a fixed mathematical equation assumed to apply throughout the sample space, nonparametric multiplicative regression relies on the data to generate local models, with the model form specified using a local multiplicative smoothing function (McCune 2006b). For our data, we used a local mean estimator and Gaussian weighting function in a forward stepwise regression, in which data points closer to the target point received greater weight. A cross-validated R^2 (xR^2) was used to evaluate model fit; xR^2 is more conservative than traditional R^2 because, when calculating the residual sums of squares, each individual data point is not used for calculating the estimate of the response of that point (McCune 2006b).

Table 2. Environmental variables used to develop nonparametric multiplicative regression models with *P. operculella* trap data for 2004, 2005, and 2006

Spring (11 variables)	Summer (14 variables)	Fall (14 variables)
Elevation	Elevation	Elevation
Latitude	Latitude	Latitude
Preceding fall MEAN, DEW, PPT	Preceding fall MEAN, DEW, PPT	Preceding winter MIN, DEW, PPT
Preceding winter MIN, DEW, PPT	Preceding winter MIN, DEW, PPT	Preceding spring MAX, DEW, PPT
Current spring MAX, DEW, PPT	Preceding spring MAX, DEW, PPT	Preceding summer MAX, DEW, PPT
	Current summer MEAN, DEW, PPT	Current fall MEAN, DEW, PPT

Spring refers to March, April, and May; summer refers to June, July, and August; and fall refers to September, October, and Novermber.

MEAN, mean temperature; MAX, maximum temperature; MIN, minimum temperature; DEW, dew point; PPT, precipitation.

Separate nonparametric multiplicative regression models were developed for each season of each year. The environmental variables that served as independent variables in the models are listed in Table 2. We hypothesized that elevation and latitude may play a role in every season, and they were included in all models. Elevation of each trapping site was determined by entering the geographical coordinates of each site into the free, on-line *GPS Visualizer* elevation lookup utility (www.gpsvisualizer.com/elevation). We also examined three types of variables related to weather: temperature, dew point, and precipitation.

Weather data from 23 weather stations located in the region where *P. operculella* trapping occurred were used for the analysis; 15 of the 23 weather stations were part of AgWeatherNet, Washington State University's Washington Agricultural Weather Network (http://weather.wsu.edu/), and 8 weather stations were associated with AgriMet (http://www.usbr.gov/pn/agrimet/), the Pacific Northwest Cooperative Agricultural Weather Network, a satellite-based network of automated weather stations located in irrigated agricultural areas throughout the Northwest, which are operated and maintained by the U.S. Bureau of Reclamation. We determined the closest weather station to each trap site using Euclidean distances, and weather variables for each season consist of daily recordings at the weather station closest to the trap location averaged over 3 mo. Locations of weather stations and 2005 trapping sites are shown in Fig. 1. The average number of traps (±SE) associated with each weather station was 9.7 ± 1.2. The average distance (±SE) from the traps and their associated weather station was 10.8 ± 0.5 km, and thus variables measured by weather stations did not reflect small scale differences among trapping locations. Similar to the weather analysis described above, we used average daily temperature to characterize summer and fall, maximum daily temperature for spring, and minimum daily temperature for winter. Dew point was examined because it indirectly measures relative humidity, and precipitation was chosen because of its impact on relative humidity and potential effect on plant growth. Each model includes weather variables that occurred during the season in which *P. operculella* was trapped, but also includes previous seasons' weather conditions. Models examining spring responses in *P. operculella* included not only spring weather conditions but also the preceding fall and winter conditions, because fall and winter conditions could potentially have a large impact on spring *P. operculella* numbers. Summer models examined not only summer conditions, but also the preceding fall, winter, and spring, and fall models took into account not only fall conditions, but the previous summer, spring, and winter temperatures, dew points, and precipitation.

Sensitivity analysis was used to determine the relative importance of the environmental variables in final, selected nonparametric multiplicative regression models (McCune 2006a, b). For each data point, a range of values of environmental variables was examined to explore the resulting changes in *P. operculella* numbers measured. The accumulation of sensitivity values across all data points were averaged and expressed as a proportion of the range of *P. operculella* numbers. A value of 1 indicates equal change in the response of *P. operculella* trap numbers per unit change in an environmental variable; a value of 0 indicates that change in an environmental variable had no effect on numbers of insects trapped. Statistical significance of models was evaluated using a Monte Carlo randomization test (McCune 2006a), in which the values of the response variable were randomly shuffled and used in the original model, and the fit was calculated. Each simulation was run 100 times, and the *P* value was calculated as the proportion of randomization runs that resulted in an equal or better fit than the original model (McCune 2006a).

Results

Yearly Trends for the Fully Deployed Trapping Network. Yearly trends in the lower, middle, and upper Columbia Basin are shown in Fig. 2. Because the trapping network was not deployed until May 2004, spring trends for that year are not known. However, mean number of males trapped in late summer and fall of 2004 in the lower Basin were substantially higher than the same period in 2005 and 2006 (Fig. 2a). In addition, 2005 had higher trapping rates than 2006 in spring, summer, and fall for every week except for two (Fig. 2a). In the middle Columbia Basin, overall trapping rates were much reduced compared with the lower Basin. Mean weekly trapping rates in the middle Basin were almost always <10 males per trap per week, and differences between years were not large (Fig. 2b). Unlike the lower Basin, the middle Columbia Basin did not show the highest trapping rates in fall 2004; rates were equally high or higher in fall 2005. In addition, July trapping rates in 2005 were slightly higher than in 2004 and 2006. The upper Columbia Basin, in contrast, showed similar trends to the lower Basin, albeit at much lower trapping rates (Fig. 2c). Fall trapping rates were higher in 2004 than in 2005 or 2006. Trapping rates in the upper Columbia Basin for fall 2004 were higher than those found during the same season and year in the middle Columbia Basin.

Yearly Trends for the Off-Season Trapping Network. Trapping rates for the nine traps active in winter 2004/2005 were among the highest recorded in the Columbia Basin for any year or season; in late November and December, trap rates were >40 males per trap per week every week and up to 152 males per trap per week in mid-December (Fig. 3). In contrast, the 11 traps active in winter 2005/2006 showed very low trapping rates for the entire off-season period (Fig. 3).

Weather Conditions. The relationships of mean temperature (average for fall and summer, maximum for spring, and minimum for winter), monthly precipitation, and dew point from 2003 to 2006 relative to the 6-yr means for each variable from 1993 to 1999 are shown in Fig. 4. In fall 2003, which preceded the serious outbreak of *P. operculella* of spring 2004, average temperature in October was significantly warmer than the reference period (1993–1999), and precipitation varied from being significantly greater than the reference period in September to significantly lower in October and November. Dew point in November 2003 was significantly lower than the reference period. In winter 2003/2004, minimum temperature was significantly lower than the reference period in January, precipitation was significantly higher in December, and dew point varied from being significantly lower in January to significantly higher in February. In spring 2004, maximum temperature was significantly higher in March and April and precipi-

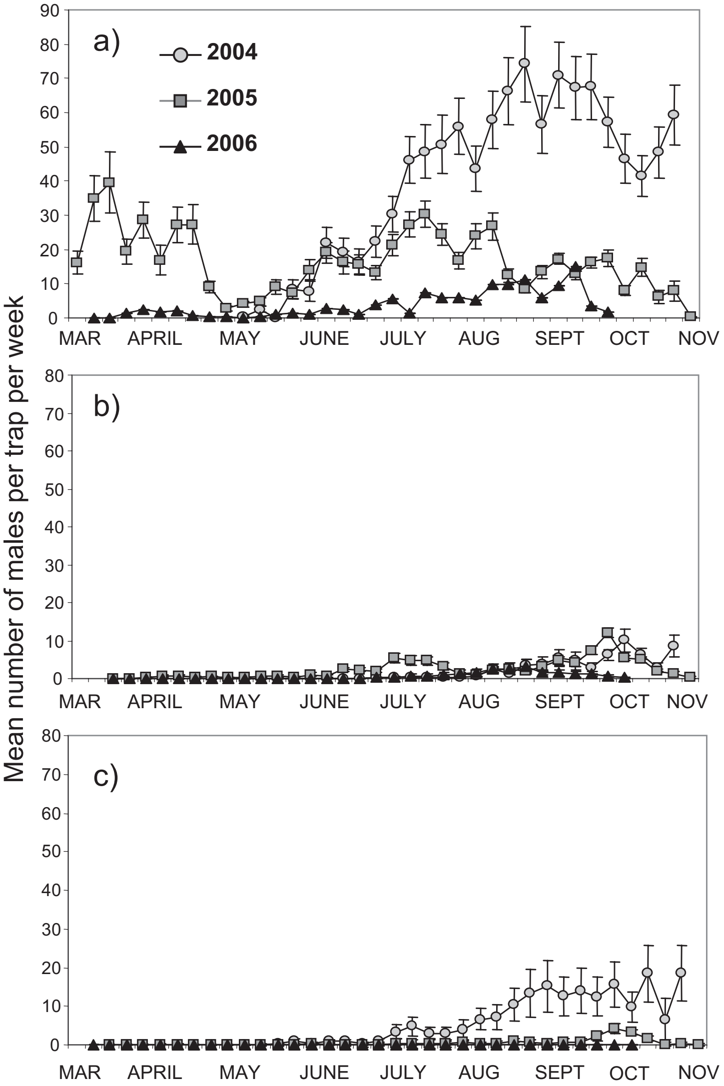

Fig. 2. Mean number (±SEM) of *P. operculella* males per trap per week during spring, summer, and fall, when the entire monitoring network was active, in the (a) lower, (b) middle, and (c) upper Columbia Basin. The geographic boundary of each region is defined in the text. Trapping in 2004 did not begin until 14 May.

tation was significantly lower in March than the reference period. Summer 2004 also had significantly higher average temperatures in June, July, and August than the reference period, and precipitation varied from being significantly greater than the reference period in June and August to significantly lower in July.

In fall 2004, average temperature was significantly higher than the reference period in October, and precipitation was significantly lower in October and November (Fig. 4). In winter 2004/2005, minimum temperature was significantly lower than the reference period in February, and precipitation was significantly lower in January and February. The dew point in winter 2005 varied from being significantly higher than the reference period in December to significantly lower in January and February. In spring 2005, the maximum temperature in March was significantly higher than the reference period. In summer 2005, the average temperature in August was significantly higher than the reference period, precipitation was significantly lower in June and July, and dew point was significantly lower in June, July, and August.

In fall 2005, average temperature was again significantly higher in October compared with the reference period, and dew point was significantly lower in September (Fig. 4). In winter 2005/2006, minimum temperature was significantly lower than the reference period in December and February and significantly higher in January. Precipitation was higher than the reference period in December and lower in February, and dew point varied from being significantly

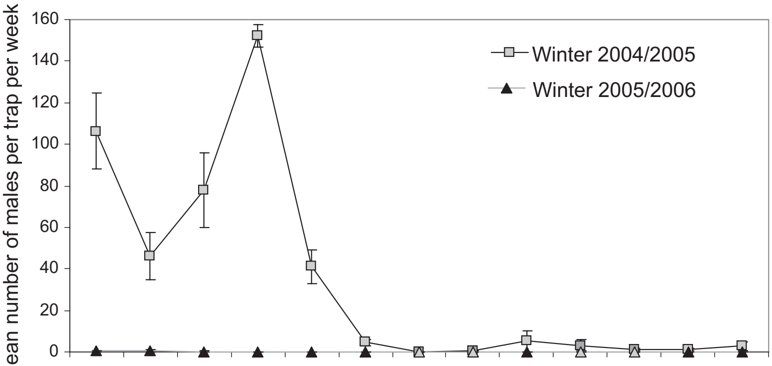

Fig. 3. Mean number (±SEM) of *P. operculella* per trap per wk in Oregon during winter 2004/2005 (n = 9 traps) and 2005/2006 (n = 11 traps).

lower in December and February to significantly higher in January. Spring 2006 had significantly lower dew points than the reference period in March and significantly higher precipitation in April. In summer 2006, average temperature in June and July was significantly higher than the reference period in June and July, and precipitation and dew point was significantly lower in July and August.

Spatial Distribution. The spatial distribution of *P. operculella* in spring, summer, and fall of 2004, 2005, and 2006 is shown in Fig. 5. The distribution of the pest in spring 2004 is the result of <2 wk trapping data and therefore is not included in later analyses. In all years, the number of trapping sites with the highest infestation levels occurred in fall. Although the highest mean number of males per trap in the growing season was recorded in 2004 in the lower Basin (Fig. 2a), the 2005 growing season had more widespread moderate to intense infestations of *P. operculella* (i.e., > 30 males per trap; Fig. 5).

Nonparametric Multiplicative Regression Model Results. Final nonparametric multiplicative regression models for each season with their sensitivities, xR^2, and P values are shown in Table 3. Final models were selected when the addition of an extra variable did not explain an additional 3% or more of the variation. Final models explained between 28 and 73% of the variation in the response variable, with five of the models having two variable solutions and three models having three variable solutions (Table 3).

Elevation and the maximum spring temperature together explained a large portion of the spatial variation in trap numbers in summer 2004 (Table 3). Traps located at lower elevations were associated with higher capture rates, with elevations >320 m associated with very few to no *P. operculella* trapped (Fig. 6a). In addition, traps at locations with higher maximum temperatures in the preceding spring were associated with higher capture rates (Fig. 6a). In fall 2004, a three-variable model including latitude, average summer temperature, and fall precipitation explained 74% of the variation (Table 3), with traps located in areas with higher summer temperatures, lower latitudes, and lower fall precipitation associated with higher capture rates (Fig. 6b and c).

In 2005, spring precipitation, the average temperature of the previous fall, and elevation explained 62% of the variation (Table 3). Elevation showed the same pattern as the previous year, and spring trap numbers were positively related to average temperature of the previous fall (Fig. 7a). Traps at locations with more spring precipitation were also associated with higher capture rates, except at elevations >320 m, where few, if any, *P. operculella* were captured (Fig. 7b). Elevation and average summer temperature explained trap numbers in summer 2005 (Table 3), with elevation showing the same pattern as previous seasons' and with locations with higher summer temperatures associated with higher trapping rates (Fig. 7c). Fall 2005 patterns (Fig. 7d) were similar to spring 2005 (Fig. 7b); trap numbers were influenced by elevation and spring 2005 precipitation in the same manner.

In 2006, the spatial distribution of spring trapping numbers was best explained by spring maximum temperature and dew point (Table 3). Traps at locations with higher spring maximum temperatures and lower dew points were associated with higher trapping rates (Fig. 8a). Dew point and elevation were also important in explaining summer 2006 trap patterns (Table 3), with lower dew points and elevations associated with high trapping rates (Fig. 8b). The fall model included elevation, summer dew point, and spring maximum temperature (Table 3), with similar trends as in previous seasons: lower elevation, higher temperatures in the previous spring, and a drier summer associated with higher trap numbers (Fig. 8c and d).

Discussion

The monitoring data showed that the highest trapping rates in the Columbia Basin occurred in 2004, when weekly trapping rates in the lower Columbia Basin rose to >70 males per trap per week (10 male per trap per day) in the fall and >140 males per week (20 males per trap per day) in December. Although the lower Columbia Basin always had the highest trapping

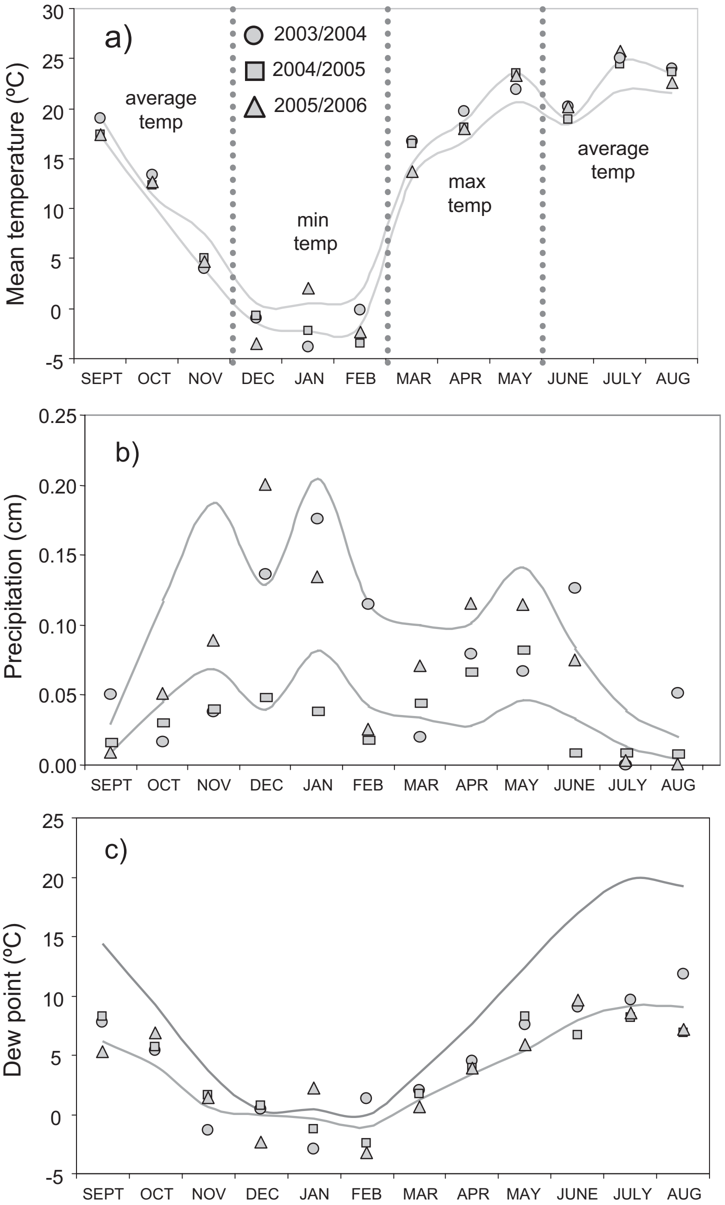

Fig. 4. Mean (a) temperature, (b) precipitation, and (c) dew point for each month of the 2003/2004, 2004/2005, and 2005/2006 trapping years. Average daily temperatures are used for fall and summer means, maximum daily temperatures are used for spring means, and minimum daily temperatures are used for winter means; see text for details. Curved gray lines represent the upper and lower limits of the 95% confidence interval for the 6-yr mean (1993–1999) of each variable.

rates in the growing season, the upper Columbia Basin had high or higher trapping rates than the middle Basin in 2004. This was surprising as our initial expectation was that more northern locations, with cooler temperatures, would be less prone to infestation. Because the highest trapping rates occurred in the lower Basin in 2004, it might be surmised that 2004 had the most severe infestation. However, if we use the spatial extent of moderate to high infestation (defined here as >30 males per trap per week) as the most important criterion, 2005 would be judged as having the most serious infestation of the 3 yr examined in this study (Fig. 5).

The trapping rates reported here seem to be lower than many rates published for other geographical regions, although differences in trap types, trap location relative to the host crop, and/or pheromone blends make comparisons to other studies difficult. Nevertheless, a study in New Zealand that used delta traps similar to the ones used in this study found daily trapping rates of 30 moths per trap during the growing season (Herman et al. 2005). In California, Shelton and

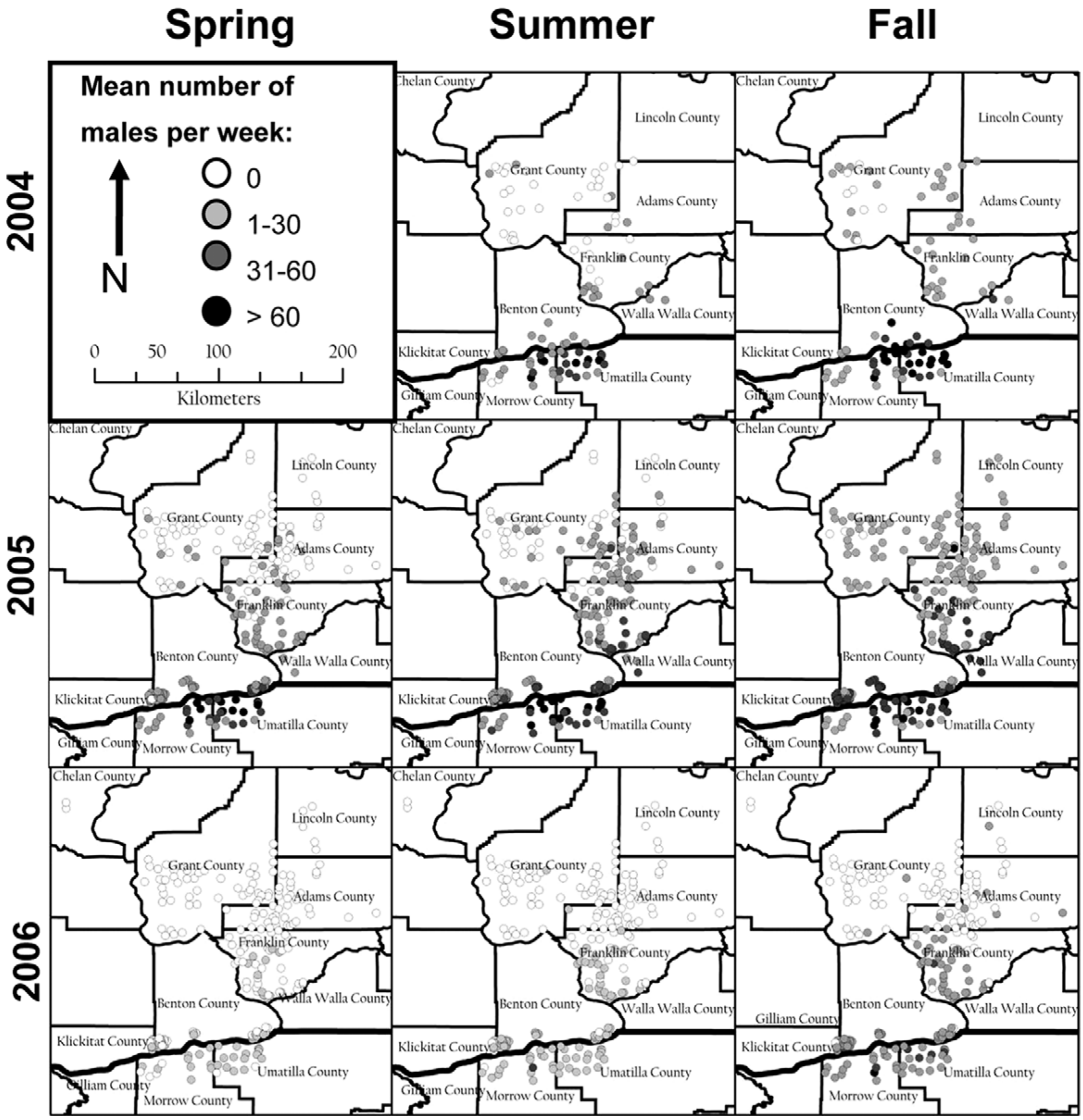

Fig. 5. Spatial distribution of *P. operculella* in spring, summer, and fall in 2004, 2005, and 2006. No data are presented for spring 2004 because only 2 wk of trapping data were availabe.

Wyman (1979) reported daily trapping rates during the growing season ranging from 10 to 279 moths per trap. However, they used pheromone-baited water pan traps in their study. Herman et al. (2005) studied the impact of different trap types in monitoring *P. operculella* in New Zealand and found that pheromone-baited water traps caught four times more *P. operculella* than delta traps. If this ratio is used to convert Shelton and Wyman's pan trap rates to delta trap "equivalents" (2.5–70 males per trap per day), their catches would still be generally higher than those reported here. Keller (2003) studied population dynamics of *P. operculella* in Peru, Kenya, and Egypt using baited, modified water traps (Raman and Booth 1983) and found weekly trap rates during major infestations to range in the thousands (up to 12,000 moths per trap) in Peru, into the hundreds for Egypt, and from the hundreds to thousands in Kenya. Thus, even though rates are difficult to directly compare, it seems clear that the trapping rates of *P. operculella* associated with the infestation in the Columbia Basin of Oregon and Washington is of a lower magnitude than many areas within its range.

One factor that may have contributed to low trapping rates in our study is that, even though traps were adjacent to irrigated crop circles (on average, 0.05 km), because of crop rotation, not all fields were planted in potato every year. Thus, not all traps were directly adjacent to potato crops each year of the study. Regardless, the rates reported here were asso-

Table 3. Nonparametric multiplicative regression model results for seasonal spatial distribution of *P. operculella* trap numbers in 2004, 2005, and 2006

	Environmental variables	Sensitivities[a]	xR^2; *P; n*
2004			
Summer	Elevation, spring 04 MAX	0.97, 0.78	0.73; $P < 0.01$; 100
Fall	Latitude, fall 04 PPT, summer 04 MEAN	0.98, 0.52, 0.12	0.74; $P < 0.01$; 97
2005			
Spring	Spring 05 PPT, fall 04 MEAN, elevation	0.33, 0.24, 0.17	0.62; $P < 0.01$; 228
Summer	Summer 05 MEAN, elevation	1.05, 0.49	0.73; $P < 0.01$; 228
Fall	Elevation, spring 05 PPT	0.69, 0.58	0.50; $P < 0.01$; 228
2006			
Spring	Spring 06 MAX, spring 06 DEW	0.69, 0.36	0.28; $P < 0.01$; 219
Summer	Elevation, spring 06 DEW	0.39, 0.38	0.40; $P < 0.01$; 228
Fall	Elevation, SU 06 DEW, spring 06 MAX	0.78, 0.24, 0.23	0.42; $P < 0.01$; 222

Spring refers to March, April, and May; summer refers to June, July, and Aug.; and fall refers to Sept., Oct., and Nov.

MEAN, mean temperature; MAX, maximum temperature; DEW, dew point; PPT, precipitation.

[a] Sensitivities reflect the relative importance of the environmental variables, with a value of 1 indicating equal change in the response variable per unit change in an environmental variable and a value of 0 indicating that change in an environmental variable had no effect on the response variable.

ciated with widespread tuber damage and large economic losses in the Columbia Basin (Rondon et al. 2007) and represent a serious threat to U.S. potato production. Even limited infestations in a field can result in large economic losses; processing plants in the region established a zero tolerance for *P. operculella* larvae in tubers because larvae are considered to be a foreign material (Rondon et al. 2007) and so an entire field can be rejected because of one larva-infested tuber. At this time, the relationship between trap numbers and tuber damage has not been established for the pest in the Columbia Basin potato production region, so trap numbers cannot be related to an economic threshold.

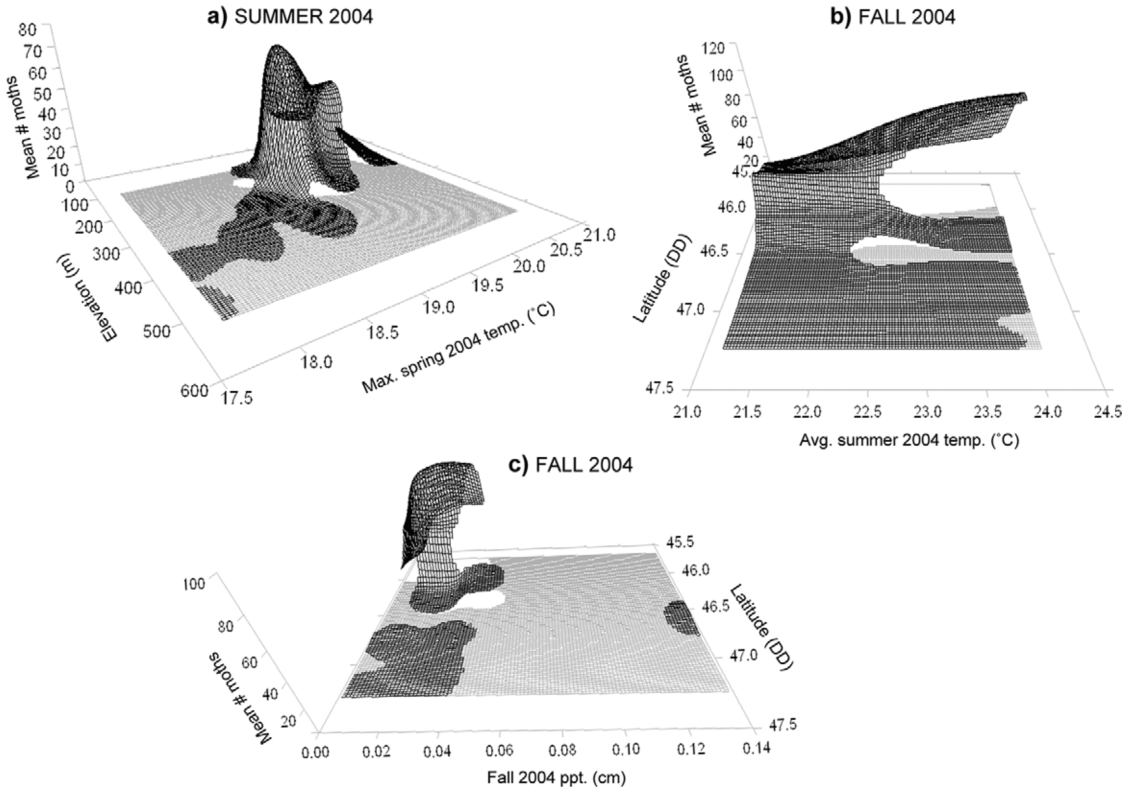

Fig. 6. Results of nonparametric multiplicative regression for (a) elevation and preceding spring maximum temperature effects on summer 2004 trap numbers, (b) latitude and average preceding summer temperature on fall 2004 trap numbers, and (c) latitude and precipitation on fall 2004 trap numbers. Two graphs are presented for fall 2004 because the model included three variables (see Table 3). Gray areas on graph indicate areas with no data. The vertical axis label "mean # moths" is per trap per week.

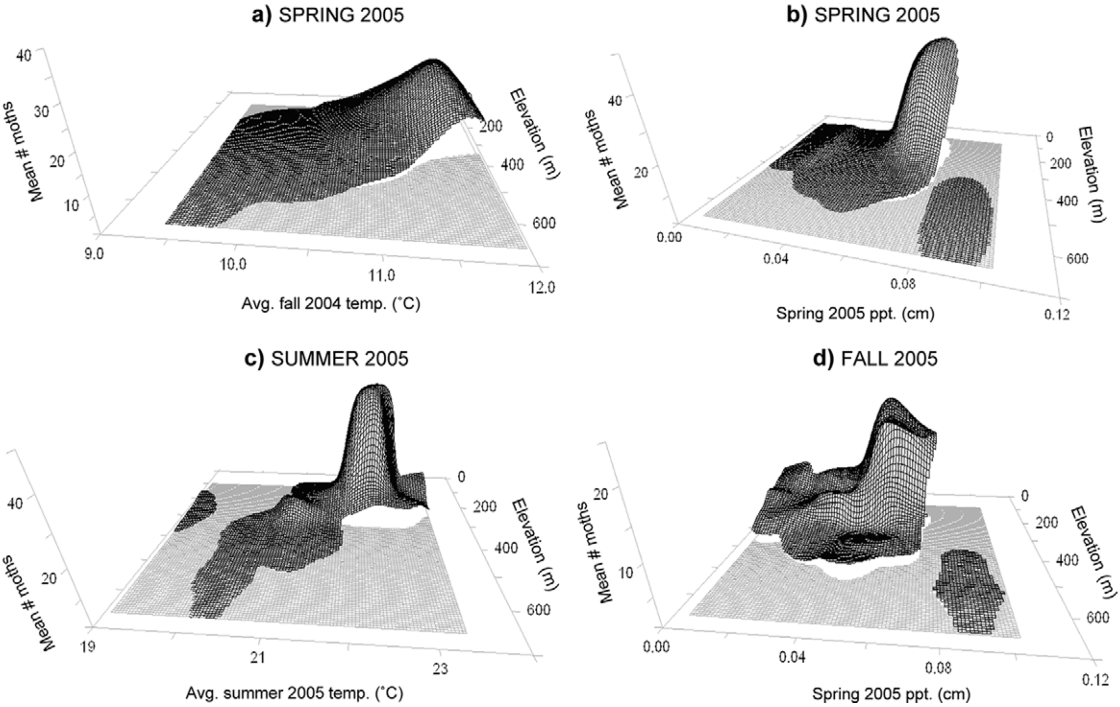

Fig. 7. Results of nonparametric multiplicative regression for (a) elevation and fall 2004 temperature effects on spring 2005 trap numbers, (b) elevation and spring precipitation effects on spring 2005 trap numbers, (c) elevation and average summer temperature on summer 2005 trap numbers, and (d) elevation and preceding spring precipitation on fall 2005 trap numbers. Two graphs are presented for spring 2005 because the model included three variables (see Table 3). Gray areas on graph indicate areas with no data. The vertical axis label "mean # moths" is per trap per week.

The record of Chittenden (1913) of *P. operculella* in the Pacific Northwest and the presence of museum specimens from the region collected in the early 1900s allow for the possibility that the pest may have existed in the Pacific Northwest for almost a century at low numbers or in isolated populations. At the very least, evidence, such as observations of Chittenden (1913) and the newspaper account of the Idaho outbreak in the 1940s described in the introduction, suggests that the pest has been introduced to the region several times. However, not until 2002 did it begin to establish itself at damaging levels. Several hypotheses exist about why the Columbia Basin has experienced the recent damaging outbreak of *P. operculella,* including the suggestion that weather changes in the region have resulted in a more hospitable environment for the pest. The severity of winter has long been believed to be an important limiting factor to the distribution of *P. operculella*, and accordingly, many studies have examined the effect of temperature and winter conditions on *P. operculella* survival and development (Graf 1917; Underhill 1926; Poos and Peters 1927; Langford 1934; Broodryk 1971; Briese 1980, 1986; Whiteside 1985; Lal 1987; Doğramaci et al. 2008). Thus, an obvious weather-related hypothesis explaining *P. operculella*'s relatively sudden occurrence as a pest in the region, especially given widespread concerns of global climate change, is warmer winter temperatures. Our data do not support this hypothesis. January minimum temperatures in the winter preceding the growing season with the highest trapping rates of *P. operculella* (2004) were significantly lower than the 6-yr average (1993–1999) before *P. operculella* was recorded as a pest in the region. February 2005 minimum temperatures were also significantly lower than the 1993–1999 reference period, yet infestations in the 2005 growing season were also high and more widespread than the previous year. In addition, the highest numbers of *P. operculella* recorded in this study occurred in December 2004 (Fig. 3), when temperatures averaged below 0°C, indicating that low temperature alone did not result in high mortality for adults, at least. The relative cold hardiness of *P. operculella* in this region is supported by Doğramaci et al. (2008), who showed that pupae in the Columbia Basin could survive winter conditions for up to 2 mo at soil depths of 6 cm when ambient temperatures averaged 0°C. Soil temperatures at 6 cm depth and greater were up to 2°C warmer in winter.

An alternative hypothesis to the milder winter one is that weather-related changes in spring, summer, and fall are more important in explaining the outbreak of *P. operculella* because these changes may have (1) resulted in more optimal conditions for the pest's growth and survival during the growing season and/or (2) reduced mortality by effectively shortening the duration of winter (rather than by reducing its severity). Our data are consistent with this hypothesis. In fall 2003, October was significantly warmer, and October and November were significantly drier than the

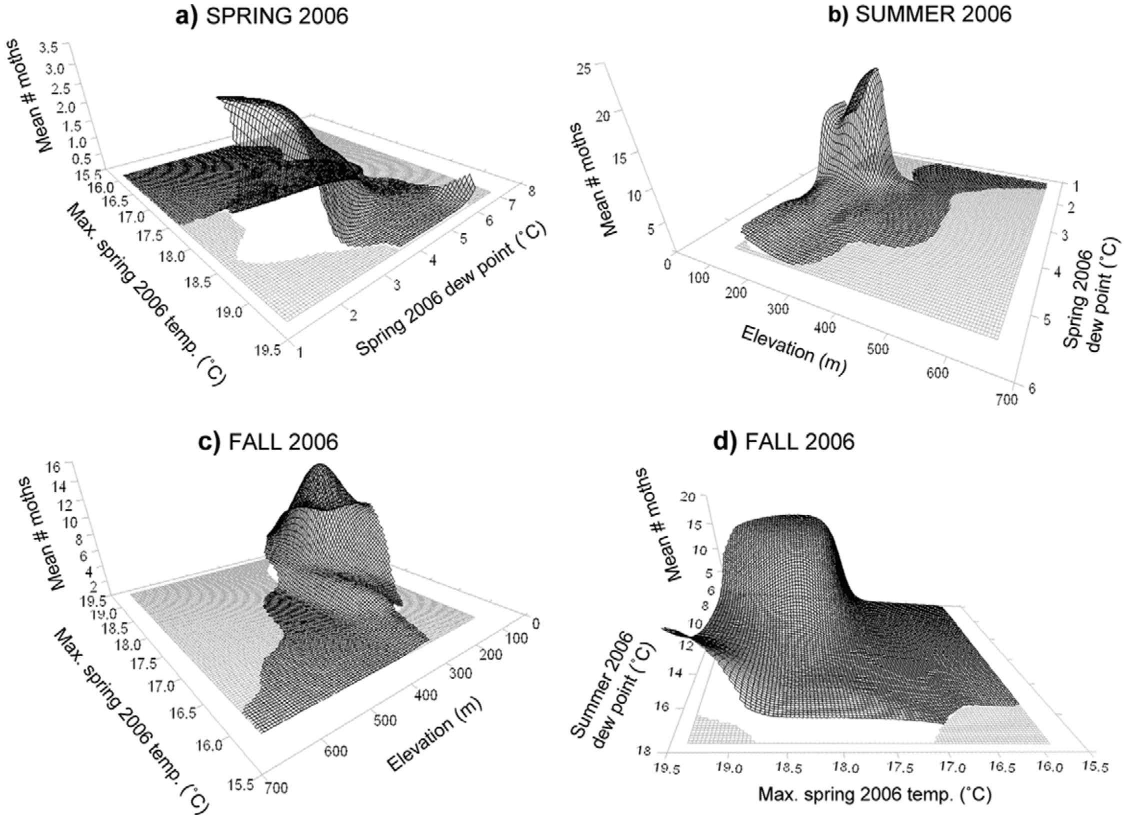

Fig. 8. Results of nonparametric multiplicative regression for (a) elevation and latitude effects on spring 2006 trap numbers, (b) elevation and preceding spring maximum temperature effects on summer 2006 trap numbers, (c) latitude and average preceding summer temperature on fall 2006 trap numbers, and (d) latitude and precipitation on fall 2006 trap numbers. Two graphs are presented for fall 2006 because the model included three variables (see Table 3). Gray areas on graph indicate areas with no data. The vertical axis label "mean # moths" is per trap per week.

1993–1999 reference period. In the following spring (2004), March and April were also significantly warmer, and March was drier than the reference period. Furthermore, all three summer months and October 2004 were warmer than the reference period, and July, October, and November had significantly less precipitation. The growing season of 2005 started out with higher temperatures in March, and the entire summer was characterized by lower dew points, less precipitation in June and July, and higher temperatures in August compared with 1993–1999. June and July 2006 were also warmer than usual.

Other studies have found that higher temperatures, up to a threshold, are associated with faster development or increased survival of *P. operculella* (Broodryk 1971; Briese 1980, 1986; Keller 2003). Thus, warm spring, summer, and fall temperatures should accelerate development of *P. operculella,* allowing for shorter generation time and more rapid population increase. In addition, relatively warmer conditions in fall and spring may effectively shorten the winter and substantially increase survival of *P. operculella.* Doğramaci et al. (2008) found that all immature stages (eggs, larvae, and pupae) experienced higher mortality with longer exposures to winter field conditions in the Columbia Basin. No larvae could survive 43 d of winter conditions, and although eggs and pupae survived up to 63 and 91 d (respectively) in winter conditions, mortality increased significantly with duration of exposure.

The spatial distribution of *P. operculella* varied both by season and by year (Fig. 5); fall showed the highest trap rates each year and 2005 had more widespread moderate to high infestations in the growing season than 2004 and 2006. All nonparametric multiplicative regression models, except for spring 2006, explained 40% or more of the variation in the response variable (i.e., *P. operculella* trapping rate; Table 3). The low xR^2 in spring 2006 was not surprising given the fact that there was little variation in the response variable because trapping rates were uniformly low (Fig. 5). The regression analyses showed that the environmental factors explaining spatial distribution of trapping rates varied depending on year and season. However, elevation was an important factor in six of the eight models (Table 3) and showed a consistent pattern in that traps at elevations >320 m were associated with low trapping rates. Thus, elevation seems to play a major role in constraining *P. operculella's* spatial distribution. In contrast, latitude was a factor in only one significant model, indicating that it plays a limited role in the distribution of *P. operculella* in this region.

Interestingly, results from the nonparametric multiplicative regression models support the idea that weather conditions in spring, summer, and fall are important factors impacting trapping rates of *P. operculella.* In summer 2004, as trapping rates increased rapidly and the spatial distribution spread (Fig. 5), spring maximum temperature (along with elevation) explained 73% of the variation in trapping rate distribution. Locations with maximum spring temperatures above 18.5°C were associated with much higher summer trapping rates (Fig. 6a). In fall 2004, summer temperature and fall precipitation were both important factors (along with latitude) explaining 74% of the variation, with high trapping rates being associated with higher temperatures and lower rates of precipitation (Fig. 6b and c). Temperature also played a role in 2005; traps at locations with higher fall 2004 temperature were associated with higher spring capture rates and traps at locations with higher summer temperatures were associated with higher summer capture rates. In contrast to all other trends showing that warmer and drier conditions were associated with higher trap numbers, spring precipitation was positively associated with spring and fall trapping numbers in 2005. One explanation for this trend may be that locations that received more precipitation in spring had more rapid growth of volunteer potatoes, resulting in earlier availability of foliage for *P. operculella* and more rapid population growth. In 2006, spring maximum temperature played a role in spring trap numbers, and spring and summer dew points were also important throughout 2006, with drier trap locations associated with higher trapping rates.

Thus, both the examination of yearly patterns in *P. operculella* infestation for 3 yr and the nonparametric multiplicative regression models generally support the idea that warmer and drier conditions, in general, increase the likelihood of having high pest pressure of *P. operculella.* The ability of nonparametric multiplicative regression analyses to examine interactions of environmental factors was important because certain factors, such as elevation and latitude, were particularly important in modulating the response of other variables. The results of this study agree, in part, with the study of Krambias (1976) examining the relationship of *P. operculella* trapping rates to trends in environmental variables. He found that daily catch rate of adults decreased with higher relative humidity in Cyprus, although, unlike the results reported here, he found no effect of temperature on catch rate. In addition, he found a weak positive relationship with increased wind speed and trap catches. The results of this study are also consistent with various laboratory studies that have shown a positive effect of either increased temperature (up to the lethal threshold) and/or decreased humidity on development and/or survival of *P. operculella* (Broodryk 1971; Briese 1980, 1986; Keller 2003).

Although both an examination of the yearly trends in weather data and *P. operculella* numbers and the nonparametric multiplicative regression analyses of spatial distributions each season suggest the importance of temperature, precipitation, and dew point, there are obvious difficulties in relating environmental variables to pest numbers in managed agroecosystems. One major limitation is posed by the fact that agricultural producers are actively attempting to reduce pest numbers by increased pesticide applications and improved cultural control methods. In addition, many variables other than those measured vary with spatial distribution. These include farm ownership (and therefore potentially agronomic practices), degree of isolation from other potato fields, and the crop currently in rotation. These factors have undoubtedly weakened the relationship of environmental variables to *P. operculella* infestation in the Columbia Basin. For example, chemical control efforts may be the most logical explanation for the differences in *P. operculella* population trajectories in the lower Columbia Basin in July 2004 and 2005. In 2004, trapping numbers from July onward continued to steadily increase throughout fall. In contrast, in July 2005, even though the trajectory until that time looked very similar, numbers declined steadily (Fig. 2a). Although no data are available on the amount of insecticides applied to control *P. operculella,* the threat posed by this pest to potato production was more widely recognized than the year before and certainly led to increased chemical control efforts. Not only might this explain the divergence in population trajectories between July 2004 and 2005, but it might also explain the fact that nonparametric multiplicative regression models for fall 2005, and all of 2006 explained less variation in trap numbers than the previous four seasons. More aggressive control efforts in summer and fall 2005 may, in turn, have reduced the overwintering population in 2005/2006. Virtually no males were trapped in winter 2005/2006 (Fig. 3).

Survival through the winter may have also been impacted by minimum temperatures that were lower than the reference period in December 2005 and February 2006. In addition, temperatures in spring 2006 were not higher than the reference period (unlike the two previous springs), which may have resulted in an effectively longer winter. Better sanitation practices may have reduced cull potato piles and harvest leftovers, thereby reducing food availability for *P. operculella* larvae in spring. All of these factors could have contributed to lower trapping numbers in all parts of the Columbia Basin in spring 2006. Continued aggressive chemical and cultural control methods may have maintained *P. operculella* at low numbers throughout the summer and fall 2006, even though temperatures were again higher than normal in June and July.

Because we have a limited sample size of 3 yr, further research is needed to study the importance of environmental factors identified in this study, including additional years of monitoring data, as well as modeling efforts that take into account life history attributes, such as lower developmental temperature thresholds. However, certain factors were shown to be potentially important by both the temporal and spatial analyses, including spring, summer, and fall temperatures. Understanding which environmental variables are important in increasing risk of serious *P. operculella* damage is an important first step in reducing that risk.

This study also presents evidence consistent with the idea that *P. operculella* may become a more serious pest in regions traditionally thought to be outside of its range if climate change results in even relatively small changes in temperature or moisture regimens.

Acknowledgments

We thank D. Batchelor, G. Dahlberg, B. Giles, A. Harris, C. Kimoto, K. Knox, M. Martin, and C. Royer for collecting and counting *P. operculella* in pheromone-baited traps; C. Smithhisler, C. Guedot, and D. Green for technical assistance in providing lures; K. Tanner for creating maps and compiling weather data; D. Wooster for reviewing this manuscript; and D. Herms for helpful advice. J. Johnson of the University of Idaho's W. F. Barr Entomology Museum, C. Marshall of the Oregon State University Arthropod Collection, and R. Zack of Washington State University's James Entomological Collection provided information about *P. operculella* specimens in their collections. Weather data were provided courtesy of Washington State University's AgWeatherNet and U.S. Bureau of Reclamation Agrimet weather networks. Funding for this research was provided by the Washington State and Oregon Potato Commissions, J.R. Simplot, ConAgra Foods, and the USDA–ARS. Suggestions by P. Tobin and two anonymous reviewers improved the manuscript.

References Cited

Bacon, O. G. 1960. Control of the potato tuberworm in potatoes. J. Econ. Entomol. 53: 868–871.

Briese, D. T. 1980. Characterisation of a laboratory strain of the potato moth, *Phthorimaea operculella* (Zeller). Bull. Entomol. Res. 70: 203–212.

Briese, D. T. 1986. Geographic variability in demographic performance of the potato moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) in Australia. Bull. Entomol. Res. 76: 719–726.

Broodryk, S. W. 1971. Ecological investigations on the potato tuber moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae). Phytophylactica 3: 73–83.

Chittenden, F. H. 1913. The potato-tuber moth. U.S. Dep. Agric. Farmer's Bull. 557: 1–7.

Doğramaci, M., S. I. Rondon, and S. J. DeBano. 2008. The effect of soil depth and exposure to winter conditions on survival of the potato tuberworm, *Phthorimaea operculella.* Entomol. Exp. Appl. 129: 332–339.

Graf, J. E. 1917. The potato tuber moth. U.S. Department of Agriculture, Washington, DC. Bull. No. 427.

Herman, T.J.B., J. R. Clearwater, and C. M. Triggs. 2005. Impact of pheromone trap design, placement and pheromone blend on catch of potato tuber moth. N. Z. Plant Protect. 58: 219–223.

Jensen, A., S. J. DeBano, N. David, M. Martin, and D. Batchelor. 2005. Tuber moth survey, April 2005. Potato Prog. 5: 1–2.

Johnson, D. A., T. F. Cummings, P. B. Hamm, R. C. Rowe, J. S. Miller, R. E. Thornton, G. Q. Pelter, and E. J. Sorensen. 1997. Potato late blight in the Columbia Basin: an economic analysis of the 1995 epidemic. Plant Dis. 81: 103–106.

Keller, S. 2003. Integrated pest management of the potato tuber moth in cropping systems of different agro-ecological zones, pp. 41–89. *In* J. Kroschel (ed.), Advances in Crop Research, vol 1. Margraf Verlag, Weikersheim, Germany.

Krambias, A. 1976. Climatic factors affecting the catches of potato tuber moth *Phthorimaea operculella* (Zell.) (Lepidoptera, Gelechiidae) at a pheromone trap. Bull. Entomol. Res. 66: 81–85.

Lal, L. 1987. Winter survival of the potato tuber moth, *Phthorimaea operculella* (Zeller), in potato fields in India. Crop Res. 27: 111–117.

Langford, G. S. 1933. Observations on cultural practices for the control of the potato tuberworm, *Phthorimaea operculella* (Zell.). J. Econ. Entomol. 26: 135–7.

Langford, G. S. 1934. Winter survival of the potato tuber moth, *Phthorimaea operculella* Zeller. J. Econ. Entomol. 27: 210–213.

McCune, B., and M. J. Mefford. 2004. HyperNiche. Multiplicative habitat modeling. Version 1.0. MjM Software, Gleneden Beach, OR.

McCune, B. 2006a. Non-parametric habitat models with automatic interactions. J. Veg. Sci. 17: 819–830.

McCune, B. 2006b. Nonparametric multiplicative regression for habitat modeling. (http://www.pcord.com/NPMRintro.pdf).

Poos, F. W., and H. S. Peters. 1927. The potato tuber worm. Va. Truck Exp. Sta. Bull. No. 61. Virginia Truck Experiment Station, Norfolk, VA.

Radcliffe, E. B. 1982. Insect pests of potato. Annu. Rev. Entomol. 27: 173–204.

Raman, K. V., and R. H. Booth. 1983. Evaluation and technology for integrated control of potato tuber moth in field and storage. Technology evaluation series no. 10. International Potato Center (CIP), Lima, Peru.

Rondon, S. I., S. J. DeBano, G. H. Clough, P. B. Hamm, A. Jensen, A. Schreiber, J. M. Alvarez, M. Thornton, J. Barbour, and M. Doğramaci. 2007. Biology and management of the potato tuberworm in the Pacific Northwest. Pacific Northwest Ext. Publ. No. 594. Oregon State University, Corvallis, OR.

Scott, D. W. 1992. Multivariate density estimation: theory, practice, and visualization. John Wiley, New York.

Shelton, A. M., and J. A. Wyman. 1979. Seasonal patterns of potato tuberworm moth *Phthorimaea operculella* abundance as determined by pheromone trapping California. Environ. Entomol. 8: 541–543.

Shelton, A. M., and J. A. Wyman. 1980. Postharvest potato tuberworm population levels in cull and volunteer potatoes and means for control. J. Econ. Entomol. 73: 8–11.

Sporleder, M., J. Kroschel, M.R.G. Quispe, and A. Lagnaoui. 2004. A temperature-based simulation model for the potato tuberworm, *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae). Environ. Entomol. 33: 477–486.

Trivedi, T. P., and D. Rajagopal. 1992. Distribution, biology, ecology and management of potato tuber moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae): a review. Trop. Pest. Manag. 38: 279–285.

Underhill, G. W. 1926. Studies of potato tuber moth during the winter of 1925–26. Va. Exp. Sta. Bull. No. 251. Virginia Polytechnic Institute, Blacksburg, VA.

Whiteside, E. F. 1985. An adaptation to overwintering in the potato tuber moth, *Phthorimaea operculella* (Zeller) J. Entomol. Soc. South Afr. 48: 163–167.

Received 25 October 2008; accepted 18 September 2009.