Occurrence of Resistance in *Uncinula necator* to Triadimefon, Myclobutanil, and Fenarimol in California Grapevines

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ABSTRACT

Gubler, W. D., Ypema, H. L., Ouimette, D. G., and Bettiga, L. J. 1996. Occurrence of resistance in *Uncinula necator* to triadimefon, myclobutanil, and fenarimol in California grapevines. Plant Dis. 80:902-909.

Uncinula necator subcultures from 19 vineyards in four regions in California were analyzed for sensitivity to triadimefon, myclobutanil, and fenarimol. The means of EC_{50} values to triadimefon, myclobutanil, and fenarimol of *U. necator* subcultures from a vineyard without previous exposure to demethylation inhibition (DMI) fungicides were 1.40, 0.15, and 0.13 mg/liter, respectively. The highest means of EC_{50} values were found in the Central Coast region, and frequency distributions were skewed most toward higher resistance to all three fungicides. Subcultures with high resistance levels also were present in the other regions examined. A time course study performed in one vineyard, where resistant strains were reported, demonstrated a steady and significant increase in EC_{50} values for all three fungicides during the growing season after multiple applications of triadimefon. Increased resistance to triadimefon, but not to myclobutanil and fenarimol, was maintained in early-formed ascospores released after the growing season.

Grape production in California utilizes 300,000 ha of land in virtually every agricultural production area. *Uncinula necator* (Schwein.) Burr., causal agent of powdery mildew, is the most important pathogen of grape in California. Infection of the berries interferes with fruit set and development, and causes off-flavors in wine, whereas rachis infections reduce storage life of table grapes. Coastal regions, particularly the central and south, encounter severe powdery mildew pressure annually. Some North Coast regions, the Sacramento Valley, and most of the San Joaquin Valley normally are subjected to lower disease pressure. Although grape varieties differ among these areas, temperature is the critical factor in disease development during the growing season (2). Under optimum temperature conditions of 18 to 25°C, which frequently occur in the central and south coastal regions, *U. necator* completes its asexual cycle in as little as 5 days. At 33°C, the reproductive cycle requires up to 15 days, and colonies do not survive when temperatures exceed 37°C for only a few hours (1). These latter conditions often occur in the central and southern San Joaquin Valley, and less frequently in the North Coast region.

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Accepted for publication 9 May 1996.

Publication no. D-1996-0603-06R
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Sulfur was used traditionally for powdery mildew control in California, with applications made on a 7- to 10-day schedule (4). However, the use of sulfur to control mildew has some limitations, including phytotoxicity at higher temperatures, necessity of frequent repeat applications for good control, and the impartment of off-flavors in wine. Therefore, growers switched to fungicides that inhibit sterol biosynthesis by demethylation inhibition (DMI fungicides) when they became available. In California, the DMI fungicide triadimefon (Bayleton, Bayer Corp. Agricultural Chemical Division, P.O. Box 4913, Kansas City, MO) was registered for powdery mildew control in 1982. Registration of two additional DMI fungicides, myclobutanil (Rally, Rohm and Haas Co., 727 Norristown Road, Spring House, PA) and fenarimol (Rubigan, Dow Elanco, 9330 Zionsville Rd., Indianapolis, IN), followed in 1989. During the 1985 and 1986 growing seasons, reduced efficacy of triadimefon was observed in some California vineyards (8). Fungicide resistance was suspected and later confirmed (5,9).

Consistent with the role of sexual reproduction in *Erysiphe graminis* f. sp. *hordei* in Europe, sexual reproduction and the formation of large numbers of viable ascospores also may contribute to development of increased levels of resistance (13). Ascospores, ejected in the spring from cleistothecia formed in the previous growing season, can be important sources of initial inoculum in California vineyards, especially in the coastal regions (3) and elsewhere (10). However, it was unclear to what extent selected resistance persisted during the sexual stage in *U. necator*.

Objectives of this research were to determine levels of resistance in *U. necator* populations in the different viticultural regions of California, to monitor changes in mean EC_{50} values to the three mentioned DMI fungicides in one vineyard during multiple applications of triadimefon during the growing season, and to detect differences in means of EC_{50} values to the three DMI fungicides in ascospore generations preceding and following the growing season.

MATERIALS AND METHODS

Collection and maintenance of mildew isolates. Collection of *U. necator* was performed in 19 vineyards in four viticultural regions in California during the 1990 growing season. Mildewed leaves were collected from 122 vines in five vineyards in the North Coast area, 103 vines in four vineyards in the Central Coast area, 136 vines in five vineyards in the northern San Joaquin Valley, and 108 vines in four vineyards in the southern San Joaquin Valley. Also, leaves were collected from 62 vines in an isolated, 18-year-old vineyard in Yuba County, California, unexposed to DMI fungicides. *U. necator* from each collected sample was inoculated separately onto 4- to 6-week-old Carignane grape seedlings, which had been grown in 5-cm pots inside a mildew-free greenhouse maintained at 35 to 37°C. After inoculation, seedlings and pots were placed into clear plastic tubes (7.5 cm w × 30 cm h). The bottoms of the tubes were sealed with plastic caps and the tops with a layer of paper towel held in place with a rubber band. A 6 mm × 15 cm plastic tubing was inserted through a hole in the towel and extended down to the soil line for watering in an otherwise closed system. This minimized the possibility of cross-contamination of the isolates. The inoculated plants were maintained in a growth chamber at 24°C with a 12-h photoperiod. Subjecting heterogeneous *U. necator* subcultures to leaf disk bioassays increased the probability of detecting individuals with the highest degree of resistance. The heterogeneity of the subcultures therefore allowed us to focus on the highest levels of resistance in each subculture detected by the assay.

Production of ascospore isolates. Ascospore subcultures were derived from cleistothecia collected before bud break from dried leaves on the vineyard floor. After harvest, leaves containing cleistothecia were collected from vines where conidial isolates had been collected during the cropping season. To dislodge cleistothecia, leaf collections were immersed in iced tap water and vigorously agitated. Cleistothecia were collected on a 170-mesh screen after filtrations through a 20- and a 40-mesh screen. The cleistothecia were spread onto a 9-cm Whatman no. 1 filter paper (10), which was later divided into 10 to 15 wedge-shaped pieces. Individual filter paper wedges were inverted and attached to the inside of a 150 × 15 mm petri dish lid. Young grape leaves were placed with the lower epidermis facing the inoculum source in a petri dish lined with moistened paper towel. The filter paper wedges and the grape leaves were sprayed daily for 4 days with deionized water and incubated in the dark at 20°C. After 4 days, the containers were removed from the incubator and placed under artificial light in the laboratory at 24 to 26°C for up to 16 days. Each colony developing on the leaves was considered to be a separate subculture. Conidia from each colony were inoculated separately onto Carignane grape seedlings. All inoculated plants were encased in plastic tubes and maintained as described previously.

Fungicides. A stock solution of each fungicide was made by dissolving technical grade triadimefon, myclobutanil, or fenarimol (93, 98.8, and 100% a.i., respectively) in acetone. The stock solutions were maintained at –12°C. Dilutions were made in deionized water prior to use for each bioassay. The acetone concentration in the aqueous solutions never exceeded 1% (vol/vol).

Leaf disk bioassay. A leaf disk bioassay was used to determine DMI sensitivity of the mildew isolates. Carignane grape seedlings were grown in a mildew-free greenhouse maintained at 35 to 37°C. Beginning 4 to 6 weeks after sowing, fully expanded leaves were excised and 11-mm leaf disks were cut with a cork borer and placed in deionized water for 1 to 2 h. Individual leaf disks were placed upside down in a petri dish on a single layer of paper towel and sprayed to runoff with an aqueous solution of one of five concentrations of each fungicide. This treatment resulted in submersion of the leaf disks in the pooled fungicide solution for approximately 30 s. The five fungicide concentrations used to determine the final EC_{50} values depended on the sensitivity of each subculture as determined by an initial assay, but ranged between 0.01 and 50 mg/liter for fenarimol and myclobutanil, and 0.01 and 100 mg/liter for triadimefon.

Leaf disks were placed, adaxial surface up, in 60 × 15 mm petri dishes lined with two layers of paper towel and two layers of Miracloth (Calbiochem Corp., P.O. Box 12087, San Diego, CA) moistened with 1 ml of water. Individual leaf disks served as experimental units. For each subculture and fungicide concentration, four leaf disks were placed in one petri dish, serving as four replicates. Fungicide-treated and water-treated control leaf disks were allowed to dry for 18 to 24 h. Petri dish lids were removed, and the dishes containing the leaf disks treated with all three fungicides as well as the control were placed randomly in a 120-cm-high settling tower. For each subculture inoculation, conidia were tapped from six to eight seedlings bearing approximately 2-week-old and heavily sporulating colonies. The settling tower was sprayed with 95% ethanol between each subculture inoculation procedure. After inoculation, the petri dishes were closed and placed in sealed, clear plastic boxes (30 × 22 × 10 cm), the bottoms of which were lined with moistened paper towel. The boxes were maintained under fluorescent light at 24°C for 10 days. Petri plates with leaf disks treated with one fungicide at one concentration were confined to one plastic box to avoid effects on mildew growth due to vapor action of the fungicides. Leaf disks were evaluated for percent surface area colonized using a Horsfall-Barratt rating system. Percent inhibition was determined by comparison to untreated, inoculated leaf disks. The EC_{50} values to the fungicides of each subculture were determined by probit transformation of the percentage of inhibition and regression against the natural logarithm of the fungicide concentrations used. In subsequent studies, the standard error of the mean of EC_{50} values of monoconidial isolates averaged approximately 20% after three repetitions of a modified bioassay (H. L. Ypema and W. D. Gubler, *unpublished*). Baseline EC_{50} values for triadimefon, myclobutanil, and fenarimol were determined for the *U. necator* population collected from the Yuba County vineyard, hereafter referred to as wild-type (WT) population. Means were calculated from EC_{50} values of subcultures collected in each viticultural region. The population median for each region was analyzed for differences with respect to the WT population by means of Wilcoxon-Mann-Whitney's two-sample test. The probability threshold was 0.0125 to correct the experimentwise error for multiple comparisons.

Time course study. Grape leaves with cleistothecia were collected from a vineyard floor in Monterey County in the Central Coast region of California on 22 January 1990. Thirty ascospore-derived subcultures from cleistothecia were used to determine EC_{50} values to the DMI fungicides. During the growing season, 30 more conidial subcultures were collected after each of four triadimefon applications (Bayleton 50 WP, 285 g a.i./ha) on 4 May, 25 June, 24 July, and 3 September. Cleistothecia were collected from leaves on 23 October 1990 to generate 30 more ascospore-derived subcultures. EC_{50} values were transformed to their natural logarithms prior to statistical analysis to increase normality of the distributions and to stabilize variances at each collection date. Regression analysis was performed separately for each fungicide with the day of the year as independent variable and the ln-transformed EC_{50} values as dependent variable. Regression was performed only on the data from January, May, June, July, and September. The data obtained in October were not included in the regression analysis because the collection at this date represented a potentially different population. This population was created after genetic recombination, which as such may have caused a nonlinear response in development of mean EC_{50} values. The ln-transformed EC_{50} values for the ascospore-derived collections from January and October were analyzed separately for each fungicide for significant differences by means of the two-sample t test with a 0.05 probability threshold. Since the data obtained for triadimefon were not distributed normally, analysis was also performed with the Wilcoxon-Mann Whitney two-sample test with a 0.05 probability threshold.

RESULTS

Figure 1 illustrates the location of each California region where *U. necator* subcultures were collected. Figures 2, 3, and 4 illustrate the frequency distributions and means of EC_{50} values in the examined regions for triadimefon, myclobutanil, and fenarimol, respectively. The WT mildew population was sensitive to low concentrations of the DMI fungicides, with mean EC_{50} values of 1.40, 0.15, and 0.13 mg/liter to triadimefon, myclobutanil, and fenarimol, respectively. The WT EC_{50} frequency distribution for all three fungicides on a logarithmic scale most closely resembled a normal distribution. The mean

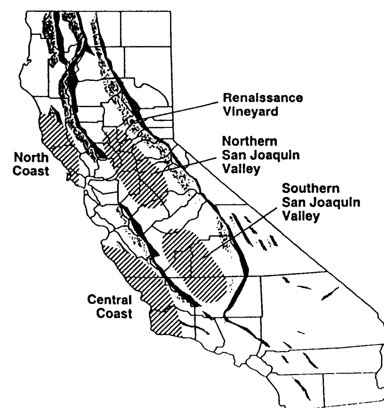
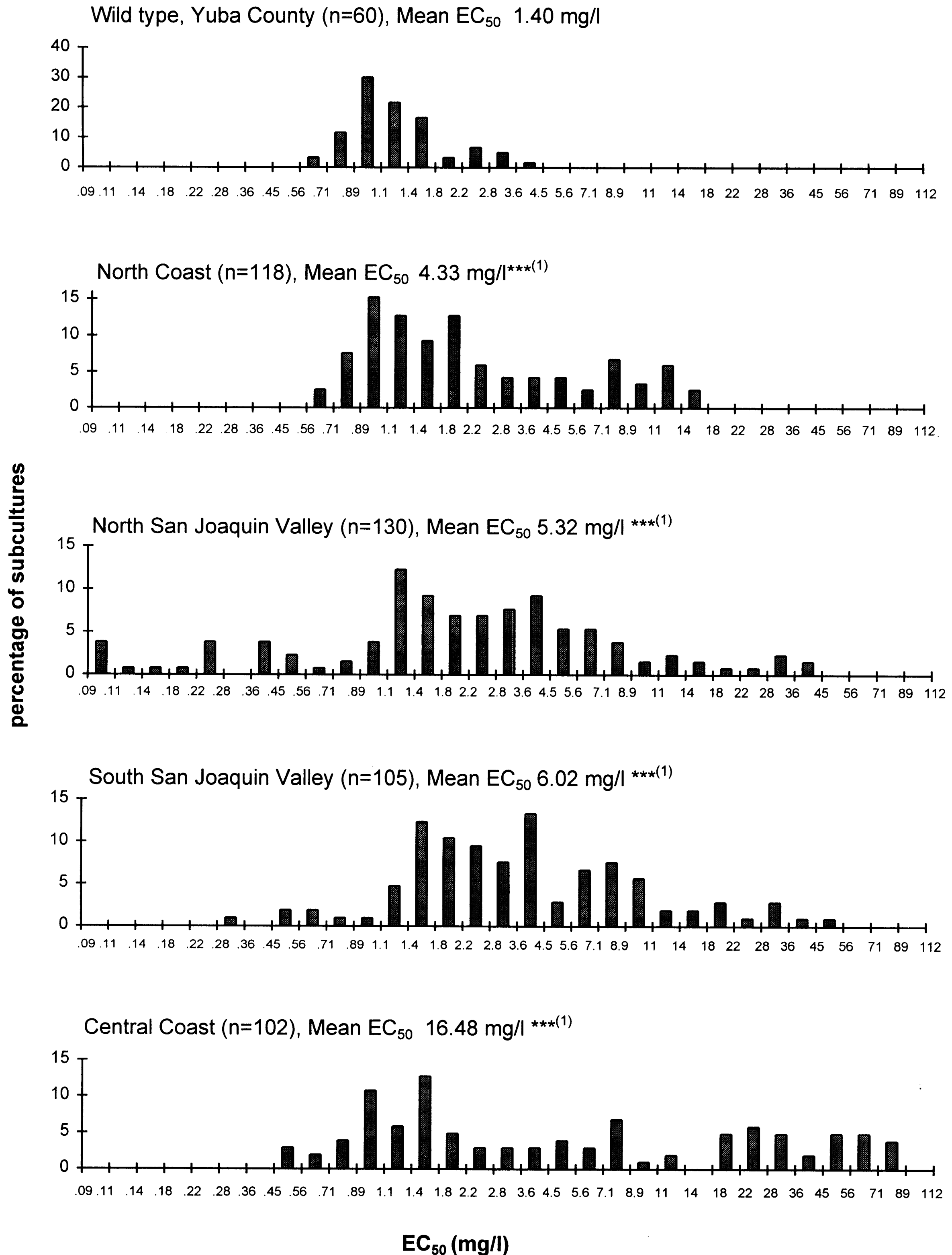


Fig. 1. Location of viticultural regions in California where *Uncinula necator* isolates were collected.

of EC_{50} values of the North Coast population was 4.33 mg/liter to triadimefon. The means of EC_{50} values to triadimefon for the northern San Joaquin Valley, southern San Joaquin Valley, and the Central Coast were 5.32, 6.02, and 16.48 mg/liter, respectively. Frequency distributions for populations in the former three regions were all skewed toward higher EC_{50} values, indicating a higher proportion of subcultures with higher resistance levels in comparison to the WT population. The Central Coast population had the largest frequency of subcultures with higher resistance levels and demonstrated the high-

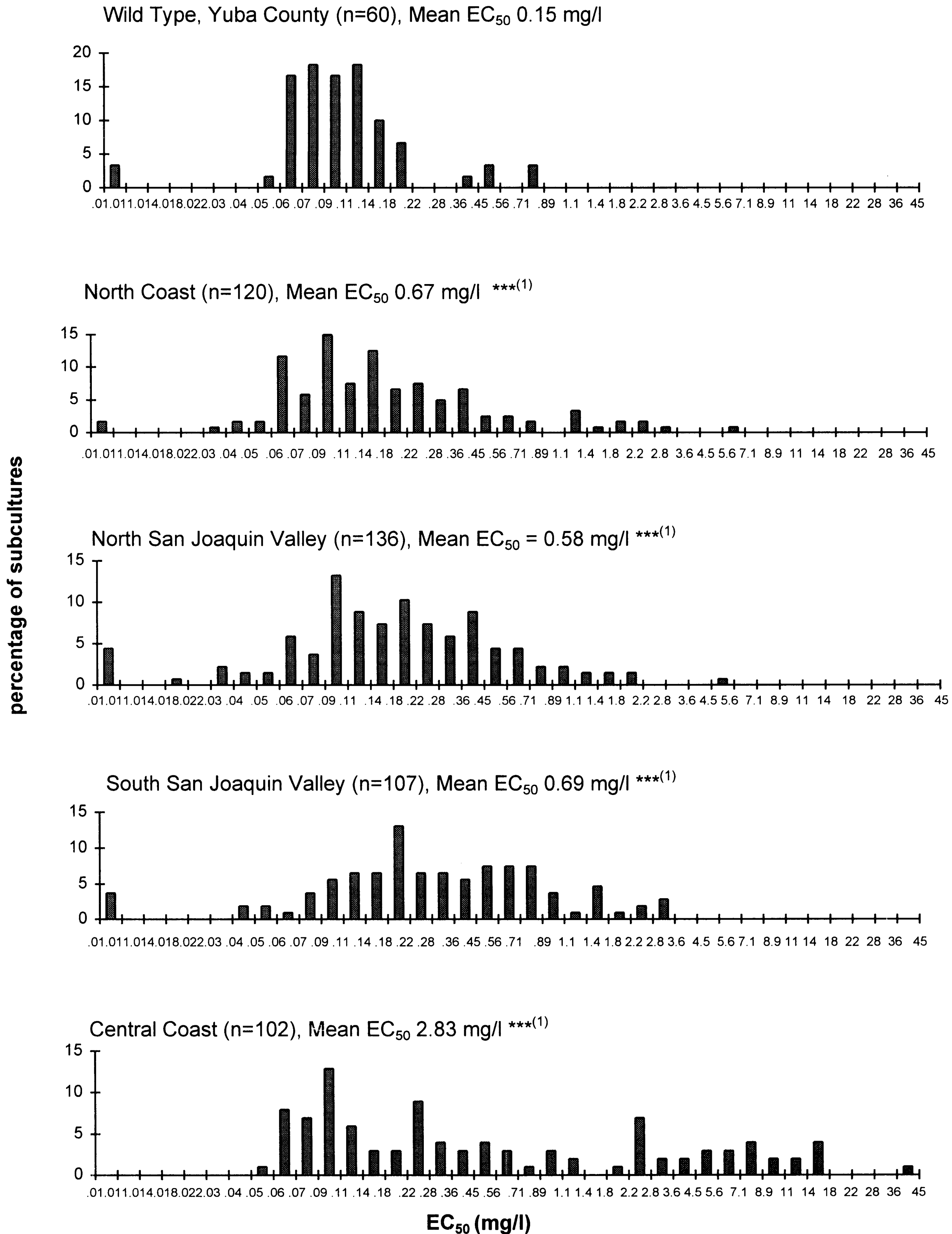


1) *** Median significantly different from the wild type population median according to Wilcoxon-Mann-Whitney's two sample test (α = 0.0125).

Fig. 2. EC_{50} frequency distributions to triadimefon for *Uncinula necator* subcultures collected in five regions in California.

est degree of departure from the WT distribution. All tests indicated a significant difference between median EC_{50} values of the population in each region and the WT population.

The pattern found for myclobutanil in these regions was similar to that found for triadimefon, but values were at lower levels. The means of EC_{50} values were 0.67, 0.58, 0.69, and 2.83 mg/liter for the North Coast, the northern and southern San Joaquin Valley, and the Central Coast, respectively. Frequency distributions in all four regions were skewed toward higher values, and this observation was most

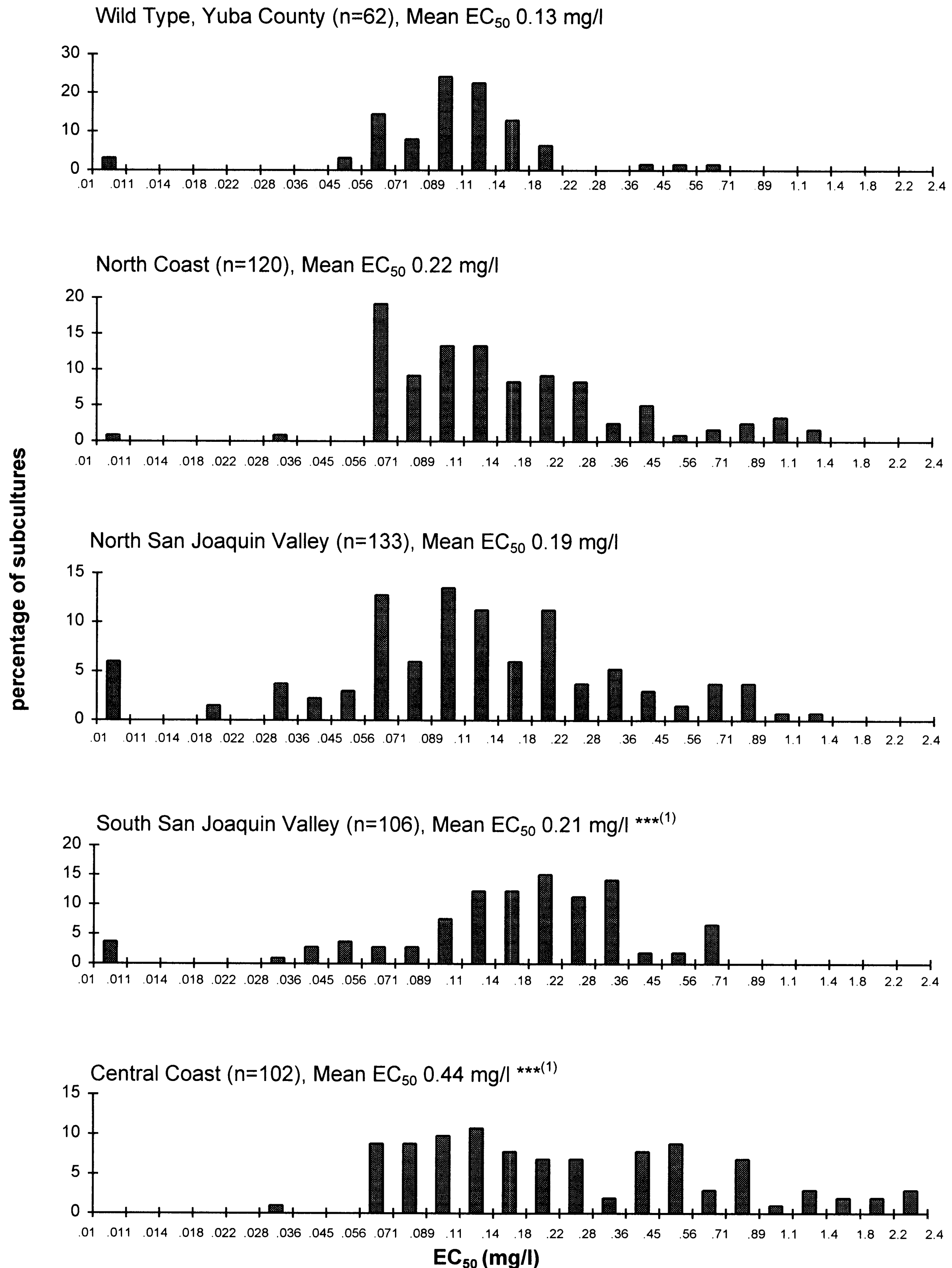


1) *** Median significantly different from the wild type population median according to Wilcoxon-Mann-Whitney's two sample test (α = 0.0125).

Fig. 3. EC_{50} frequency distributions to myclobutanil for *Uncinula necator* subcultures collected in five regions in California.

extreme for Central Coast subcultures. Similarly to observations with triadimefon, all tests indicated a significant difference between the population of each region and the WT population.

For fenarimol, the means of EC_{50} values were 0.22, 0.19, 0.21, and 0.44 mg/liter for the North Coast, the northern and southern San Joaquin Valley, and the Central Coast, respectively. The previously mentioned test indicated significant differences from the WT population only for the populations from the southern San Joaquin Valley and the Central Coast. In general, the distributions suggested a lesser degree of cross-



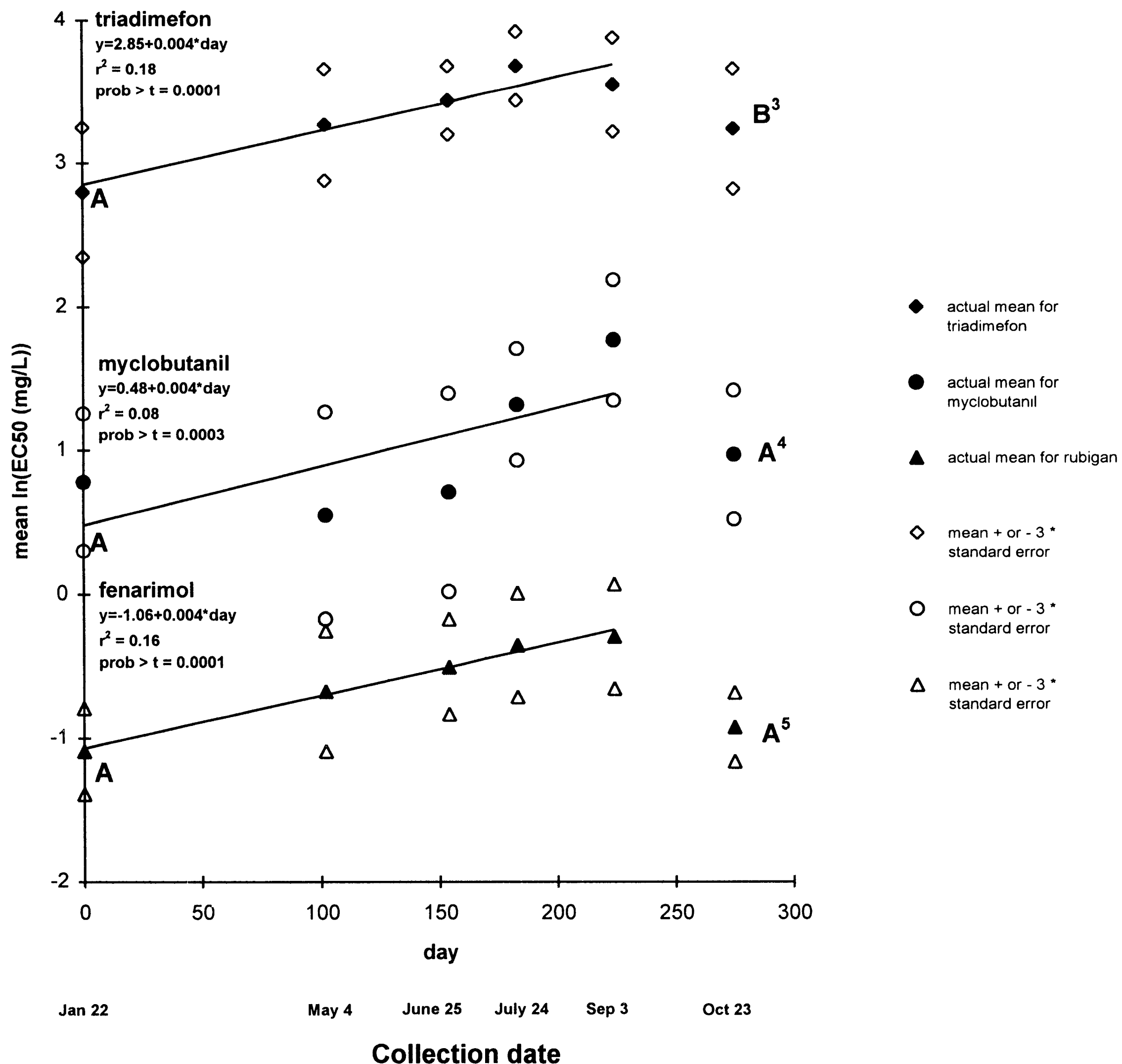
1) *** Median significantly different from the wild type population median according to Wilcoxon-Mann-Whitney's two sample test (α = 0.0125).

Fig. 4. EC_{50} frequency distributions to fenarimol for *Uncinula necator* subcultures collected in five regions in California.

resistance to fenarimol than to myclobutanil and triadimefon. Subcultures with high EC_{50} values to either fungicide were detected most frequently in the Central Coast.

Time course study. Figure 5 illustrates results of the time course study for *U. necator* collected from January to October in the Monterey County vineyard in the Central Coast region of California. Means of EC_{50} values to triadimefon, myclobutanil, and fenarimol of 30 ascospore-derived subcultures collected in January were 21.35, 3.16, and 0.41 mg/liter, respectively. Following the first application of triadimefon in May, the average EC_{50} values increased to 33.35 mg/liter for triadimefon, 3.27 for myclobutanil, and 0.69 for fenarimol. After the last application of triadimefon on 3 September, mean EC_{50} values reached a high of 54.41 for triadimefon, 7.94 for myclobutanil, and 0.94 for fenarimol. Collections from ascospores on 23 October showed means of 32.20, 3.52, and 0.43 mg/liter for triadimefon, myclobutanil, and fenarimol, respectively.

Separate regression analyses of the ln-transformed EC_{50} values against the number of days between 22 January and 23 September indicated positive slopes significantly different from zero for triadimefon, myclobutanil, and fenarimol. This indicated that levels of resistance were increasing from January through September 1990. The relatively low R^2 values reflect the wide ranges of EC_{50} values found at each collection date for each fungicide. Mean EC_{50} values of the ascospore-derived collection of October was higher than the collection of January with respect to triadimefon and myclobutanil, but the difference was significant only for triadimefon. Since the triadimefon EC_{50} values were not distributed normally, significance was confirmed by means of the Wilcoxon two-sample test. Mean EC_{50} values for myclobutanil and fenarimol obtained in January and October were not significantly different.



1. EC_{50} values were transformed to their natural logarithms prior to analysis.
2. Collections made in January and October were derived from ascospores, collections in May, June, July and September were derived from conidia.
3,4,5. Comparison of means of ln-transformed EC_{50} values of *U. necator* subcultures derived from ascospores collected in January and October 1990
3. Triadimefon:significantly different from the January collection (2-sample t-test, Wilcoxon 2 sample test, α=0.05).
4. Myclobutanil: not significantly different from the January collection (2 sample t-test, α=0.05).
5. Fenarimol: not significantly different from the January collection (2 sample t-test, α=0.05).

Fig. 5. Regression analysis for increases in EC_{50} values of *Uncinula necator* to triadimefon, myclobutanil, and fenarimol from January to September 1990, and comparison of mean EC_{50} values for ascospore-derived subcultures collected in January and October 1990.

DISCUSSION

Fungicide resistance in *U. necator* to three DMI fungicides was evaluated in four regions in California and in one isolated vineyard that had not been exposed to DMI fungicides. Although data are unavailable for fungicide sensitivity prior to use of DMI fungicides in California *U. necator* populations, the EC_{50} values determined for subcultures from the WT population presumably represent sensitivity in absence of these compounds. For the purpose of this study, the examined WT population provided us with a reference for evaluation of the populations in the other regions. The highest EC_{50} values in the WT population were 4, 0.8, and 0.6 mg/liter to triadimefon, myclobutanil, and fenarimol. Subcultures with higher EC_{50} values in the other regions were considered resistant. In the Central Coast region, disease outbreaks occur with regularity, and DMI fungicides have been a valuable tool in powdery mildew control. When triadimefon was registered for use on grapes, many growers abandoned sulfur and often used triadimefon as an eradicant at the lowest recommended rate. This may have stimulated the selection process for isolates with elevated resistance levels and contributed to a rapid increase in resistance in the population. Similar results were observed in apple orchards in which fenarimol dosages lower than the recommended rates did not control the most resistant *Venturia inaequalis* adequately (7). The repeated use of triadimefon as the sole component of mildew control programs under severe disease pressure may explain the high frequency of resistant subcultures and high EC_{50} values to this fungicide in the Central Coast region. The frequency of subcultures resistant to myclobutanil and fenarimol in the Central Coast region also appeared to be higher than in other regions. Mean and maximum EC_{50} values for myclobutanil and fenarimol were lower than those for triadimefon in all regions. Since these differences were also apparent in the WT population, they were probably due in part to a higher inherent activity of myclobutanil and fenarimol with respect to triadimefon. Subsequent work (H. L. Ypema and W. D. Gubler, *unpublished*) has not indicated considerable changes in activity of and resistance to triadimefon, myclobutanil, or fenarimol since 1990. Future investigations may reveal whether the latter observations are due to physiological limitations of *U. necator* to express higher resistances, or changes in the practiced mildew control programs and their effects on further selection of resistance, such as the reintroduction of sulfur statewide in 1987.

Subcultures with EC_{50} values to each fungicide similar to those in the Central Coast region were detected in the northern and southern San Joaquin Valley, but their numbers were lower. It is possible that normally higher summer temperatures in the San Joaquin Valley slowed the rate of asexual reproduction and the selection process for resistance. Ambient temperatures in the North Coast production areas also are often unfavorable for reproduction of *U. necator,* and disease pressure generally is less severe. Relative climatic conditions in the examined viticultural regions may explain the observed differences in DMI resistance among *U. necator* populations. Additionally, the high solar radiation levels during the growing season and natural barriers in the form of mountain ranges apparently limit long-distance movement of conidia between viticultural regions. Therefore, the regional subpopulations of *U. necator* in California may be separated more effectively than those of *E. g.* f. sp. *hordei* in Europe. There, the climatic conditions generally favor movement of inoculum over longer distances (6,13).

The time course experiment indicated a steady increase in means of EC_{50} values for all three DMI fungicides, even though triadimefon was the only applied fungicide. These results suggest that selection pressures by triadimefon can influence resistance to myclobutanil and fenarimol as well. The most likely reason for this is that the genetic mechanisms conferring resistance to DMI fungicides generally are correlated. The latter assumption is consistent with results of a study on genetic correlation of DMI resistance in *Pyrenophora teres* (11). Applications of myclobutanil and fenarimol in a section of this vineyard prior to this experiment also may have contributed to development of strains more resistant to all three DMI fungicides.

Mean EC_{50} values of the ascospore-derived subcultures to triadimefon, myclobutanil, and fenarimol were all higher than mean EC_{50} values of subcultures from the WT population. This suggests that DMI resistance can be maintained in overwintering ascospores. In the time course study, the ascospore-derived subcultures from the October collections demonstrated a mean EC_{50} to triadimefon significantly higher than the subcultures from the previous January, suggesting that increased triadimefon resistance perpetuates through the sexual cycle. However, the mean of EC_{50} values was considerably lower than that of the last conidial collection in September. Although debatable, this does not necessarily indicate that resistant strains are at a selective disadvantage during sexual reproduction, because cleistothecial formation commences in June and genetic recombination would have occurred at that time. Therefore, it is likely that most of the progeny borne in early-formed cleistothecia escaped further selection pressures from subsequent fungicide applications. Whether ascospores released from cleistothecia formed in August and September would have given rise to populations with EC_{50} values similar to those of conidial isolates collected in September requires further investigation. The results of this study show that triadimefon resistance persists during the winter in the sexual stage of *U. necator*. In areas where the fungus survives in its asexual stage in dormant grape buds (12), resistance may perpetuate also. This would provide the fungus with two avenues to maintain resistance, a situation similar to *E. g.* f. sp. *hordei* in Europe (13). In contrast to the finding with triadimefon, EC_{50} values for myclobutanil in ascospore-derived populations of October were not significantly higher than values for populations collected in January. The means of EC_{50} values of the January and October collections were similar. This suggests that an existing conidial population with increased resistance levels to the latter two fungicides found in September was either unstable or absent during the initiation of the sexual cycle in June or later. In the latter case, higher EC_{50} values would have been detected in subcultures from ascospores collected next spring. Examination of a *U. necator* population over several years may provide more information about perpetuation of resistance to each fungicide.

During the course of these studies, field trials were conducted to determine the effects of reintroducing sulfur into control programs in which its use had been discontinued. Results of these trials (W. D. Gubler and L. J. Bettiga, *unpublished*) showed conclusively that alternating sulfur with DMI fungicides in vineyards containing resistant subcultures resulted in better disease control than tank mixing DMI fungicides and sulfur, or than DMI fungicides applied by themselves. In similar field trials (W. D. Gubler, *unpublished*), triadimefon was applied at 285 g/ha at either 14-, 18-, or 21-day intervals. When triadimefon was applied at 18- and 21-day intervals, severe disease pressure was observed soon after the second application. These results led to recommendations to use DMI fungicides at maximum rates and in alternation with sulfur after every second application. Similarly to observations in *Venturia inaequalis* (7), DMI fungicides used to control *U. necator* should not be used at reduced rates and spray intervals should not be extended, even in situations where resistant strains are low in frequency. Good coverage and alternating DMI fungicides with sulfur appear to delay further development of resistance.

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