Cleistothecia of *Uncinula necator*—An Additional Source of Inoculum in Italian Vineyards

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ABSTRACT

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Density and viability of populations of cleistothecia of *Uncinula necator* from bark, leaves, and soil were determined in three vineyards in the Florence and Siena provinces of Tuscany for 3 years. A higher density of cleistothecia was found on fallen leaves than on bark. However, the percentage of viable cleistothecia was higher on bark. No viable cleistothecia were recovered from soil. *U. necator* overwintered as mycelium in dormant infected buds, which gave rise to flag shoots, only in Santa Cristina, where 20 and 92 flag shoots per hectare were detected before bloom in 1994 and 1995, respectively. Disease incidence and severity increased similarly at Corti, Fornace, and at Santa Cristina, although powdery mildew epidemics started from ascospores only in Corti and Fornace, whereas flag shoots were present at Santa Cristina. Cleistothecia were formed in autumn in both 1994 and 1995, and their dispersal started in late September to mid-October, with the maximum number of cleistothecia trapped in funnels during the second half of October. Cleistothecia appear to function as the sole source of primary inoculum for grape powdery mildew in some Italian vineyards and serve as additional sources of inoculum where the pathogen also overwinters in infected buds. In Australia but not in New York, the pathogen also overwinters as cleistothecia on fallen leaves.

Additional keywords: *Oidium tuckeri*, *Vitis vinifera*

The two principal sources of primary inoculum for grape powdery mildew, caused by *Uncinula necator* (Schw.) Burr., are mycelium within dormant buds and ascospores borne in cleistothecia. Mycelium overwintering in dormant infected buds has been considered the principal source of primary inoculum in Europe (3,12,16,20). These infected buds give rise to shoots covered with a dense colony of powdery mildew and are called flag shoots (12). Although widely reported in literature prior to 1985 to be degenerate or nonfunctional structures, cleistothecia have been shown to be the sole source of primary inoculum in New York, where flag shoots have not been observed (11). Cleistothecia have been demonstrated more recently to serve as an additional source of inoculum in California (17) and in Australia (10)—two areas where flag shoots are known to occur. Action taken to eradicate cleistothecia can reduce significantly the incidence and severity of powdery mildew (8). In New

York, and presumably in areas with similar climates, cleistothecia are dispersed to the bark of the vines by rainfall as they mature (6). Immature ascocarps that remain on leaves do not survive winter, nor do cleistothecia deposited on soil (6). In contrast, cleistothecia on overwintered leaves are an important source in comparatively low-rainfall regions in Australia, where presumably the transport of mature ascocarps from leaves to bark by autumn rains is less complete (10).

There have been few reports on the presence of cleistothecia of *U. necator* on grapevines in Europe (18–20). Cleistothecia had been observed only sporadically, and their presence was attributed to particular weather conditions occurring in certain years (3,15). Recently, cleistothecia have formed abundantly in some European regions (1,5). European reports of abundant cleistothecia have increased steadily (9,14), and there is growing concern regarding their role as a source of primary inoculum. We have occasionally observed cleistothecia in Italy on grapevines in Lombardy, Veneto, and Tuscany.

Our objectives were to determine the possible role of cleistothecia in epidemics of grape powdery mildew in Tuscany where powdery mildew epidemics are often severe and to quantify the density and viability of cleistothecia on leaves, on bark, and in the soil.

MATERIALS AND METHODS

Recovery of cleistothecia. Bark, fallen leaves, and soil were collected from two vineyards (Corti di Sotto and fattoria Santa Cristina, Tenute Antinori) in the Florence province of Tuscany on 1 March 1994, 1 March 1995, and 15 January 1996 and from another vineyard (Fornace) located in the Siena province of Tuscany on 1 March 1995 and 15 January 1996 as described by Gadoury and Pearson (6). The Corti vineyard is a planting of *Vitis vinifera* L. 'Sangiovese' and is surrounded by forests. The Santa Cristina vineyard is a planting of *V. vinifera* 'Chardonnay' within a large vine growing area. The Fornace vineyard is a planting of *V. vinifera* 'Sangiovese' and is surrounded by olive orchards. Bark was collected also on 4 May 1994 at Corti.

For each vineyard, bark was collected from the upper trunk of three vines that were cordon-trained and spur-pruned, from each of five locations that were evenly spaced along the diagonals of the vineyard. Soil from the upper 1 to 2 cm of the surface beneath the vines and leaves overwintering on the ground were collected from the same locations. Samples were air-dried in the laboratory at room temperature ($25 \pm 2^\circ\text{C}$).

Cleistothecia were recovered using the method described by Cortesi et al. (4). Thirty grams of bark or leaves were placed in a 2-L Erlenmeyer flask containing 1.5 L of water, while 100 g of soil were suspended in 1 L of water. The flask was shaken vigorously by hand for 3 min and the water was poured through nested 50- (300 μm) and 120- (125 μm) mesh Cobb sieves. The process was repeated three times, but subsequent shaking times were reduced to 1 min. After the fourth rinse, cleistothecia collected on the 120-mesh sieve were counted as described previously (4).

Twenty cleistothecia from each substrate at each location within the vineyard were transferred to a glass microscope slide and their viability was assessed with the fluorescent vital stain fluorescein diacetate as described by Cortesi et al. (4).

Disease assessments. Flag shoots were counted by examining all vines within 0.15-ha plots in Corti and Santa Cristina and within the entire vineyard at Fornace, from Eichorn and Lorenz (13) phenological stage 9 to 17 (three leaves unfolded to

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pre-bloom, respectively). In 1994, flag shoots were assessed twice at Corti and Santa Cristina, while in 1995 the assessments were performed every 10 days at Santa Cristina and Fornace.

Biweekly records of both incidence and severity of powdery mildew on leaves and fruit clusters were collected at each site in four 12-vine plots that received no fungicide applications until berries began to brighten in color (phenological stage 35, or véraison). One hundred leaves and fruit clusters were examined in each plot. Disease incidence was expressed as percentage of leaves or fruit clusters infected. Disease severity was estimated for leaves and fruit from visual keys of diseased surface area (2).

Recording weather instruments at each research site in 1994 and 1995 provided records of hourly rainfall and temperature. These were analyzed for the occurrence of ascospore release and infection events as described by Gadoury and Pearson (7), i.e., ≥ 2.5 mm rainfall coincident with temperatures $\geq 10^{\circ}\text{C}$ between the growth stages of bud break and bloom.

Dispersal of cleistothecia. Dispersal of cleistothecia was monitored using funnels, as described by Cortesi et al. (4), with minor modifications. Eight vines were randomly selected in a plot where powdery mildew was controlled with fungicides and eight vines were selected in an untreated plot. Two funnels were attached with pins to each side of the cordon on each vine (four funnels per vine). In 1994, in Corti and Santa Cristina, and 1995, in Santa Cristina and Fornace, funnels were first installed at the end of August and were replaced every 2 weeks until late-November to early December, when more than 90% of the leaves had fallen from the vines. Each funnel was examined and the number of cleistothecia was counted. Viability was assessed with the fluorescent vital stain fluorescein diacetate (4).

RESULTS

Density and viability of cleistothecia. Cleistothecia of *U. necator* were found at Corti and Santa Cristina in all 3 years of the study and at Fornace in 1995 and 1996. In 1994, the mean number of cleistothecia per kilogram of fallen leaves was 29,040 at Corti and 21,450 at Santa Cristina. On bark, the comparable values were 1,810 at Corti and 600 at Santa Cristina; whereas in soil the comparable values were 180 at Corti and 1,140 at Santa Cristina. In 1995, the mean number of cleistothecia per kilogram of fallen leaves was 5,500 at Corti and 2,400 at Santa Cristina. No fallen leaves remained on 1 March in 1995 at Fornace due to cultivation in the vineyard. In 1995, mean numbers of cleistothecia per kilogram of bark were 330 at Corti, 110 at Santa Cristina, and 68,730 at Fornace. No cleistothecia were detected in soil samples from Corti or Santa Cristina in 1995, but

400 cleistothecia per kilogram of soil were found at Fornace. In 1996, the mean number of cleistothecia per kilogram of fallen leaves was 12,260 at Corti, 92,690 at Santa Cristina, and 70,590 at Fornace. No cleistothecia were recovered from bark samples collected at Corti in 1996, but bark samples from Santa Cristina and Fornace bore 3,420 and 10,100 cleistothecia per kilogram, respectively. No cleistothecia were recovered from soil samples at any site in 1996.

Ascospores in most cleistothecia recovered from leaf samples were dead, based on their failure to fluoresce in the presence of the vital stain fluorescein diacetate. No viable ascospores were found in cleistothecia from fallen leaves at Santa Cristina in 1994 or 1995, but 10.5% (standard error

[se] = 3.7) of the cleistothecia from leaves at Santa Cristina contained viable ascospores in 1996. Viability among populations from leaves at Corti was 8.2% (se = 3.5) in 1994, 0% in 1995, and 6% (se = 0.6) at this site in 1996. As stated above, no leaves were recovered from Fornace in 1995, but viability among populations from leaves at Fornace was 8.6% (se = 5.4) in 1996.

Viable cleistothecia were not detected in soil samples at any site in any year of the study. The range of viability among populations of cleistothecia from bark was greater than that observed on leaf samples. For example, in 1994 viability was 6.4% (se = 4.4) at Santa Cristina and 27.5% (se = 3.5) at Corti. When bark from this site was sampled again on 4 May 1994, 15.3%

Table 1. Density of populations of viable cleistothecia of *Uncinula necator* on fallen leaves, bark, and in vineyard soils at three sites in Italy

Year	Substrate	Viable cleistothecia per kg substrate ^a		
		Corti	Santa Cristina	Fornace
1994	Leaves	2,378.3	0.0	nd
	Bark	497.4	38.6	nd
	Soil	0.0	0.0	nd
1995	Leaves	0.0	0.0	nd
	Bark	nd	nd	46,461.4
	Soil	0.0	0.0	0.0
1996	Leaves	735.6	9,704.6	6,035.4
	Bark	nd	1,440.8	833.3
	Soil	0.0	0.0	0.0

^a Leaves, bark, and soil were collected at each vineyard site between January and March of each year. Cleistothecia were removed from known weights of each substrates by selective sieves and counted. Viability of ascospores within cleistothecia was assayed by using the fluorescent vital stain fluorescein diacetate. nd = no data.

Table 2. Occurrence of rain events favorable for infection of grapevines by ascospores of *Uncinula necator* between the growth stages of bud break and bloom at Corti, Santa Cristina, and Fornace

Year	Dates of infection events ^a		
	Corti	Santa Cristina	Fornace
1994	18 April	16 April	nd
	21 April	5 May	nd
	22 April	9 May	nd
	29 April	18 May	nd
	1 May		
	9 May		
	18 May		
	19 May		
	25 April	23 April	27 April
1995	11 May	24 April	28 April
	12 May	30 April	10 May
	13 May	11 May	11 May
	14 May	12 May	12 May
	17 May	13 May	13 May
	18 May	14 May	14 May
	19 May	16 May	16 May
	31 May	17 May	17 May
	3 June	18 May	18 May
	6 June	19 May	31 May
	10 June	31 May	11 June
	11 June	2 June	12 June
	12 June	6 June	

^a Dates of bud break in 1994 were 16 and 18 April at Santa Cristina and Corti, respectively. Dates of bloom in 1994 were 1 and 7 June at Santa Cristina and Corti, respectively. Dates of bud break in 1995 were 22 April at Santa Cristina, and 25 April at Corti and Fornace. Dates of bloom in 1995 were 9 June at Santa Cristina, 12 June at Corti, and 15 June at Fornace. Release of ascospores from cleistothecia and infection by ascospores *sensu* Gadoury and Pearson (7) requires ≥ 2.5 mm rain coincident with temperatures $\geq 10^{\circ}\text{C}$.

($se = 10.1$) of the cleistothecia still contained viable ascospores. In 1996, 42.1% ($se = 22.9$) of the cleistothecia from bark samples at Santa Cristina contained viable ascospores. Viability could not be determined from samples of bark collected in 1995 at Corti and Santa Cristina due to insufficient numbers of ascocarps. At Fornace in 1995, 67.6% ($se = 16.6$) of the cleistothecia borne on bark contained viable ascospores, but viability on bark was only 8.3% ($se = 5.1$) at this site in 1996.

The total quantity of viable inoculum from each substrate was computed as the product of the density of the total number of cleistothecia per kilogram of substrate and the percentage of viable cleistothecia in the samples. Fallen leaves were a source

of viable cleistothecia at Corti in 1994 and at all three sites in 1996 (Table 1). The highest potential inoculum dose observed on bark occurred at Fornace in 1995 (Table 1), with lesser densities detected at Corti in 1994, at Santa Cristina in 1994 and 1996, and at Fornace in 1996 (Table 1).

Disease development. Numerous rain events favorable for ascospore release and infection occurred between bud break and bloom at Corti and Santa Cristina in 1994 and at all three research sites in 1995 (Table 2). Eight infection periods occurred at Corti in 1994, while five were recorded at Santa Cristina. Nearly twice as many infection events occurred in 1995: 14 at Corti and Santa Cristina, and 13 at Fornace (Table 2). In both 1994 and 1995, infection

periods occurred at all sites within a few days of bud break (Table 2). Intervals of 10 days or more without rain occurred in 1994 between 19 May and early June at Corti and Santa Cristina, from 19 to 31 May 1995 at Corti and Santa Cristina, and from 31 May to 11 June 1995 at Fornace.

Symptoms of powdery mildew were first detected on 4 May 1994 in Corti and Santa Cristina. At Corti, where vines had advanced to phenological stage 13 (three leaves unfolded), chlorotic spots with a metallic sheen were observed on the abaxial surface of five leaves, located at the first or second basal node of shoots. They were later confirmed as colonies of *U. necator* in the laboratory. No flag shoots were found at Corti on 4 May or in subsequent disease assessments. However, at Santa Cristina 13.2 and 19.8 flag shoots per hectare were found on 4 May and 1 June 1994, respectively.

Disease progress was similar in both vineyards (Fig. 1), despite the absence of flag shoots at Corti. Incidence of powdery mildew on leaves and fruit clusters increased to nearly 100% between 13 June and 7 July 1994. Severity of powdery mildew increased later in the growing season but reached relatively high levels on both leaves and fruit by 10 August 1994, at which time the vines had reached phenological stage 35 (Fig. 1).

No symptoms of *U. necator* were observed in Santa Cristina or Fornace on 4 May 1995. Symptoms were first observed at Santa Cristina on 15 May, when 13.7 flag shoots per hectare were detected. The number of flag shoots per hectare increased to 59.5 on 25 May and to 91.6 by 5 June. All mildew colonies observed on 15 May were located within 4 m of a flag shoot. By 25 June, all such foci had coalesced.

No flag shoots were observed at the Fornace vineyard on any assessment date. Colonies of *U. necator* were detected on 25 May 1995 at phenological stage 15 (start of elongation of inflorescence). The incidence of leaf infection increased rapidly between 15 and 25 May, while disease severity on leaves remained below 1.0% (Fig. 1). All powdery mildew colonies observed on 25 May were located on abaxial leaf surfaces of leaves at the basal three nodes of shoots. Disease increased similarly at both Santa Cristina and Fornace in 1995, despite the absence of flag shoot at Fornace (Fig. 2).

Dispersal of cleistothecia. Immature cleistothecia were first observed in early August 1994 on fruit clusters of unsprayed vines in Santa Cristina and were trapped in funnels beneath these vines between 31 August and 14 September but not in subsequent rain events (Fig. 3). Dispersal of cleistothecia from sprayed vines at Santa Cristina did not begin until the period between 12 and 28 October and continued during the interval of 28 October to 15 November (Fig. 3). Viability of cleistothecia

Fig. 1. Progress of grape powdery mildew epidemics in 1994. Incidence and severity on (A) foliage at Corti, (B) fruit at Corti, (C) foliage at Santa Cristina, and (D) fruit at Santa Cristina.

Fig. 2. Progress of grape powdery mildew epidemics in 1995. Incidence and severity on (A) foliage at Fornace, (B) fruit at Fornace, (C) foliage at Santa Cristina, and (D) fruit at Santa Cristina.

cia trapped beneath sprayed vines in Corti and Santa Cristina during the interval between 12 and 28 October was 39.7% (se = 2.06) and 57.3% (se = 1.7), respectively.

In 1995, mature cleistothecia were dispersed from untreated vines in Santa Cristina during the interval between 17 and 31 August. Dispersal from treated vines was not detected until the interval between 20 September and 4 October (Fig. 3) and continued until leaf fall in late November. In Fornace, cleistothecia were dispersed from unsprayed vines during the interval between 4 and 18 October. With the exception of the unsprayed vines at Santa Cristina in 1994, most cleistothecia were trapped during a single 2- to 3-week interval beginning in mid-October (Fig. 3). Viability of cleistothecia trapped in Santa Cristina and in Fornace between 18 October and 6 November 1995 was 39.6% (se = 11.1) and 21.4% (se = 7.9), respectively.

DISCUSSION

Cleistothecia of *U. necator* were detected in vineyard surveys at all sites in all years of our study on a variety of host tissue and substrates. Gadoury and Pearson (6) reported that the pathogen was heterothallic. Therefore, disease incidence and severity and any factor directly or indirectly affecting disease intensity thereby affects the time of appearance of ascocarps in vineyards (6). Based on our observations, we believe that the initiation and development of cleistothecia in Italian vineyards could occur in any year given suitable conditions for disease development.

Cleistothecia were dispersed to and survived winter on the bark of grapevines at all sites, although the percentage of viable cleistothecia was highly variable. Dispersal followed a period of intense disease development. Gadoury and Pearson (6) observed that peak dispersal in New York generally occurred after disease incidence had reached 100% on unsprayed vines in late August to mid-September. At our sites, the peak of dispersal generally occurred in mid-October, following the increase of foliar disease to similar levels.

Like Australia (10) and unlike New York (6), viable cleistothecia were recovered from leaf litter at our sites. Survival of overwintered leaf litter until bloom is commonplace in many Italian vineyards, although cultivation can bury much of the leaf litter before bloom. Nonetheless, the dense aggregations of cleistothecia on leaf litter make them a potentially important source of inoculum, despite the relatively low percentage of viable ascocarps observed in our study. As in Australia, autumn rains at our research sites may have been insufficient to effect the complete transfer of physiologically mature ascocarps from leaves to bark that apparently occurs in New York (6), leaving behind a residue of viable cleistothecia that

survive on fallen leaves (10). As reported by Gadoury and Pearson (6), we did not observe survival of cleistothecia in soil at our sites.

Weather conditions suitable for release of ascospores from overwintered cleistothecia occurred frequently between bud break and bloom, reportedly the seasonal period of ascospore release (6,10), in 1994 and 1995. One infection period at Santa Cristina and four infection periods at Corti occurred shortly after bud break in 1994, at least 10 days before mildew colonies were observed on 4 May. Seven infection periods occurred between bud break and 10 days before initial disease detection at Fornace in 1995. Thus at Corti and Santa Cristina in 1994 and at Fornace in 1995, there were viable cleistothecia within the vineyards, and conditions suitable for release of ascospores and infection of grapevine sufficiently early in the growing season to allow for symptom expression by the time disease was observed at the above sites.

Shoots emerging from infected buds are stunted and bear infected leaves that are heavily coated with the mycelium of *U. necator* and are thus easily found and identified as flag shoots in vineyard assessments (13). Early in their development, flag shoots serve as intense foci of infection, and secondary spread from flag shoots is easily traced to a nearby source. In contrast, ascospore infections on leaves

appear as discrete colonies, generally on the abaxial leaf surface, often near the leaf margin, and are usually randomly dispersed within vineyards (11). In our vineyard surveys, flag shoots were not observed at Corti in 1994, nor were they present at Fornace in 1995. At both of these sites, infections typical of ascospore infections were recorded. Therefore, several lines of circumstantial evidence indicate that cleistothecia are a functional and important source of primary inoculum in Italian vineyards: (i) they were formed abundantly; (ii) they were both dispersed to bark and remained resident on fallen leaves; (iii) cleistothecia survived winter and remained viable; leaf litter also remained intact on the vineyard floor; (iv) weather conditions conducive to ascospore infection occurred frequently, and were followed by appearance of typical ascospore infections in vineyards; (v) colonies typical of ascospore infections were detected in the absence of flag shoots; and (vi) at vineyard sites where only ascospore infections were detected, epidemics were equally severe when compared with sites harboring flag shoots.

Rather than the degenerate structures they were once reported to be, cleistothecia of *U. necator* have been shown to be an important source of primary inoculum, first in New York (11) and in subsequent investigations that indicated that in addition to flag shoots, they are important sources of

Fig. 3. Dispersal of cleistothecia of *Uncinula necator* in rainwater from fungicide-sprayed and unsprayed vines at (A) Corti and Santa Cristina in 1994 and (B) Santa Cristina and Fornace in 1995.

primary inoculum in California (17), Australia (10), and now Italy.

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